NEURAL CORRELATES OF EMOTIONAL MEMORY AS A FUNCTION OF AGE AND DEPRESSIVE SYMPTOMS

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NEURAL CORRELATES OF EMOTIONAL MEMORY AS A FUNCTION OF AGE AND DEPRESSIVE SYMPTOMS

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SUMMARY

Age-related positivity effects are well established in the literature. Positivity effects in memory are represented as greater benefits for positive over neutral material and/or reductions in the benefits for negative over neutral material with age. However, it is unknown if positivity effects are limited to older adults without depressive symptoms. In the current fMRI study, individuals ages 18-76 with a range of depressive symptom severity were scanned as they rated the emotional intensity of positive, neutral, and negative images that were preceded by cues to signal the valence of the upcoming image. Participants subsequently completed a recognition memory task outside of the scanner. Behavioral, univariate, representational similarity, and functional connectivity analyses provided evidence for interactive effects between age and depressive symptoms. For instance, at low levels of depression, typical patterns in aging emerged: younger age was associated with better memory for negative than neutral images, and this memory benefit for negative material was reduced with older age. With increasing levels of depression, however, there was a reduction in the positivity effect, manifesting as improvements in negative relative to neutral memory. The neural data highlighted mechanisms that may underlie these interactive effects, including reductions in prefrontal cortex functional connectivity associated with downregulation of negative affect. Together, these findings suggest that depressive symptoms in older adulthood reduce positivity effects through alterations in neural networks underlying emotion regulation.

CHAPTER 1. INTRODUCTION

While emotional content is often better remembered than neutral content across adulthood (for review, see Murphy & Isaacowitz, 2008), older age is associated with enhanced benefits for positive and reduced benefits for negative material (Carstensen & Mikels, 2005; Mather, 2012)—a pattern known as the "positivity effect" (for meta-analysis and review, see Reed et al., 2014). Preferential processing of positive over negative valence is reflected in neuroimaging work showing, for example, that older adults engage amygdala more for positive than negative events relative to young adults (for review, see Mather, 2016), and they show reduced perceptual processing of negative details (Gong et al., 2020; Mathieu et al., 2014; Mienaltowski et al., 2011). Positivity effects are frequently explained in terms of the socioemotional selectivity theory (SST; Carstensen et al., 1999; Carstensen et al., 2006). According to this theory, we operate with a set of goals throughout adulthood, but the relative importance of the various goals shifts as actual and perceived time left in life diminishes. In early adulthood, individuals may prioritize future goals as they make long-term plans for their lives. Over time, these goals realign such that priorities in late life focus on present-oriented goals such as maintaining meaningful relationships and emotional well-being. One method for promoting these goals is engagement in emotion regulation to increase positive affect and decrease negative affect (Barber et al., 2016; Carstensen et al., 2003). Emotion regulation requires recruitment of control processes such as selective attention to positive information and inhibition of goal-irrelevant negative information (see Ochsner & Gross, 2005; Ochsner et al., 2012, for review). Though cognitive control processes are known to decline with age (Braver & Barch, 2002;

Campbell et al., 2012; Gallant et al., 2020; Hasher & Zacks, 1979), the positivity effect may arise from an interaction between cognitive control and emotion regulation processes such that emotional goals are more accessible later in life, and older adults devote a larger proportion of their cognitive resources to accomplish those goals (Mather & Knight, 2005; Nashiro et al., 2012).

Emotion regulation at the neural level involves recruitment of prefrontal regions to modulate activity in emotional appraisal and perceptual processing regions (for review, see Ochsner et al., 2012). For example, positive reappraisal—a strategy older adults use effectively to regulate emotional affect—has been shown to engage lateral and medial prefrontal cortex (PFC) areas (Dore et al., 2017; Halfmann et al., 2021) often observed in cognitive control tasks. When engaging emotion regulation to reduce negative affect, this increase in PFC activity is associated with a reduction in amygdala activity (for reviews, see Berboth & Morawetz, 2021; Etkin et al., 2015). Healthy older adults have shown this inverse pattern of activity when using explicit or intentional regulation strategies (Lloyd et al., 2021; Urry et al., 2006), and when using implicit or incidental emotion regulation (for review, see Gyurak et al., 2011; Payer et al., 2012).

Our lab previously conducted a study (Corbett et al., 2020) to assess emotional memory differences between young and older adults and the mechanisms involved not only in stimulus processing, but also in anticipation of the stimulus. While undergoing scanning, participants were presented with a sound cue to indicate whether the upcoming image would be of neutral or negative valence. Participants were asked to rate the emotional intensity of the stimulus and were later given a recognition memory test outside of the scanner. Consistent with SST, older adults showed worse memory for negative than neutral

images, while young adults' memory did not differ between valence conditions. The authors connected this with the neural findings of an inverse relationship between ventromedial PFC (vmPFC) and amygdala only in older adults following negative cues, suggesting that older adults engaged spontaneous emotion regulation strategies to reduce the negative affect of the upcoming stimulus[1]. These findings are in line with other work showing amygdala activity is modulated by vmPFC regulation processes to a greater extent in older than in younger adults (Leclerc & Kensinger, 2011; Roalf et al., 2011; Sakaki et al., 2013; St Jacques et al., 2010). In addition to vmPFC, dorsomedial PFC (dmPFC) has also been associated with emotion regulation, playing a role in up- or downregulating emotional responses in the appraisal of experiences (for review, see Kensinger & Ford, 2021). Previous work has shown inverse connectivity between dmPFC and hippocampus in older adults for negative events (Ford & Kensinger, 2018), which may be related to reduced vividness of memory for negative events.

The literature reviewed thus far pertains to healthy aging. However, there is reason to believe processes underlying the positivity effect may be disrupted by symptoms of depression. Depression has been shown to impact memory for emotional events (for review, see Dillon & Pizzagalli, 2018). Individuals with depression show substantially better memory for negative than for positive or neutral material (for meta-analysis and review, see James et al., under review). A frequently cited explanation for such findings is that material which is congruent with one's mood state is better remembered than that which is incongruent (for reviews, see Holland & Kensinger, 2010; Matt et al., 1992).

[1] This conclusion was drawn from the imaging data only; participants were not explicitly asked to engage specific regulation strategies, nor were they asked about their use of regulation strategies after the task.

Onset and maintenance of negative mood states in depression have been linked to dysfunctional emotion regulation. Individuals with depression frequently use less effective or even maladaptive emotion regulation strategies, such as rumination, and have difficulty engaging the more effective strategies like reappraisal (Joormann & Stanton, 2016). Deficits in cognitive control, which are common in depression (for meta-analyses and reviews, see Dotson et al., 2020; Snyder, 2013), may at least in part underlie dysfunctional emotion regulation. For example, rumination has been linked to difficulty directing attention away from negative material (Joormann & Gotlib, 2010), which can lead to negative memory biases (LeMoult & Gotlib, 2019; Nolen-Hoeksema et al., 2008). Studies have shown that individuals with depression exhibit amygdala hyperactivity in response to negative stimuli that is not modulated by prefrontal regions the way it is in healthy controls (for meta-analysis and review, see Hamilton et al., 2012). Even when depressed individuals are able to downregulate amygdala activity comparably to controls, this ability becomes increasingly difficult with higher symptom severity (Erk et al., 2010). Similar effects have also been reported during the anticipation of negative events. For example, in Abler et al. (2007) depression severity was positively correlated with amygdala activation when participants expected a negative stimulus (but see Feeser et al., 2013, for discrepant findings, which authors suggested could be due to lower anxiety symptoms in their sample).

Few studies investigating emotional memory in depression have included older participants in their samples. Furthermore, even when studies include older adults, comparisons are often made between depressed and healthy control groups. It may, however, be more informative to assess depression as existing along a continuum because

while prevalence of diagnosed major depressive disorder (MDD) decreases with age, clinically significant symptoms of depression are believed to increase (for reviews, see Polyakova et al., 2014; Szymkowicz et al., 2019). It is therefore unclear how depressive symptoms in late life impact the positivity effect found in healthy older adults. The current study addressed these gaps in the literature, as described below.

In Corbett et al. (2020), a subsequent analysis revealed that young adults had significantly more symptoms of depression (though none had been clinically diagnosed at the time of study) compared to older adults. Because depression is known to impact emotion regulation, the authors could not rule out the possibility that young adults' failure to downregulate negative affect was due to their depressive symptoms. Furthermore, because they only used negative and neutral images in this study, the researchers could not test whether older adults also showed greater memory benefits for positive relative to neutral images than the young—a pattern that would provide additional support for the positivity effect. Finally, an unanswered question from this study concerns the age at which these spontaneous regulation processes emerge. The design used in the current study expands on that used in Corbett et al. (2020) to elucidate these uncertainties and investigate the interactive effects of age and depressive symptoms on memory for emotional events and the underlying neural processes. While undergoing scanning, participants ages 18-76 with a range of depressive symptom severity rated the emotional intensity of positive, neutral, and negative images that were preceded by audio cues to signal the valence. Participants then completed a recognition task for the images outside of the scanner.

I predicted the memory benefit for negative events should be reduced with age, and the memory benefit for positive events should increase with age, in line with SST. I

predicted these relationships would be weaker with higher levels of depression, which would support the idea that depressive symptoms reduce the positivity effect in older adults. To investigate how age and depression uniquely and jointly affected stimulus processing, I analyzed full trials using univariate and representational similarity analyses (RSA) in regions of interest (ROIs). These ROIs consisted of bilateral anatomical amygdala, ventral occipitotemporal cortex (VOTC), hippocampus, and orbitofrontal cortex (OFC), as well as functional dmPFC (see Method for details). Similar to the behavioral predictions, I expected age-related positivity effects to be reduced with higher levels of depression. In the univariate analyses, I predicted this would take the form of reductions in preferential processing of positive images and/or increases in processing of negative images. To the best of my knowledge, the current study uses RSA in a novel application to address the research questions, thus the predictions are somewhat exploratory. It has been suggested that better memory for a category is associated with greater pattern similarity between events from the same category and greater pattern dissimilarity between events from different categories (Sommer & Sander, 2021). Thus, the positivity effect may be represented as neural patterns for positive events looking more like patterns for other positive events than like patterns for neutral events. Therefore, it was expected that higher level of depression in older age would be associated with a reduction in the specificity of neural patterns associated with positive events and/or an increase in the specificity of neural patterns associated with negative events. To investigate emotion regulation, I assessed functional connectivity during catch trials using generalized psychophysiological interaction (gPPI) analyses. Seed regions in vmPFC and dmPFC were selected based on findings in prior work of their role in exerting regulatory control to increase or decrease

activity in other regions. Specifically for these analyses, I examined connectivity between the seed regions and amygdala (separately for left and right hemispheres due to prior findings of lateralization for different types of regulation; for review, see Barreiros et al., 2019; Vrticka et al., 2011), VOTC, and hippocampus. I predicted that higher level of depression in older age would be associated with diminished upregulation of positive affect and downregulation of negative affect.

CHAPTER 2. METHOD

2.1 Participants

Participants were 72 individuals, ages 18-76. Participants were recruited between May 2019 and March 2021 from Georgia Institute of Technology and the Atlanta community via flyers and an advertisement placed on public transportation. Sixteen of these participants were excluded: three due to computer malfunction, three due to excessive movement during scanning, one due to a large discrepancy in depression scores between initial phone screening and in-person assessment (46 vs. 0), two due to low performance on cognitive assessments (MMSE scores = 24 and 21; MoCA scores = 14 and 16), one participant could not stay awake in the scanner, one had low trial counts due to slow responses, and four stopped before the end of the scanning session. The remaining 56 participants (24 females; mean age 40.55 ± 16.99 years; mean education 14.73 ± 2.38 years; race: 41.1% White/Caucasian, 39.3% Black/African-American, 7.1% Asian, 7.1% multiracial, 1.8% Middle Eastern, 1.8% Pacific Islander, 1.8% Hispanic/Latinx; ethnicity: 80.4% not Hispanic/Latinx, 7.1% Hispanic/Latinx, 12.5% not indicated) were included in the behavioral and fMRI analyses. While education was not correlated with age ($r(56) = -.08$, $p = .54$), depressive symptomology (as measured by the CES-D) was negatively related to age ($r(56) = -.32$, $p = .02$; see Figure 1). Education and depressive symptoms were not significantly correlated ($r(56) = -.07$, $p = .59$).

All included participants were right-handed, native English speakers, with normal or corrected-to-normal vision, and were without history of CNS or cardiac disease. Participation was compensated with class credit or $15 per hour, plus an additional $5 for

travel expenses. All participants signed consent forms approved by the Georgia Institute of Technology institutional review board.

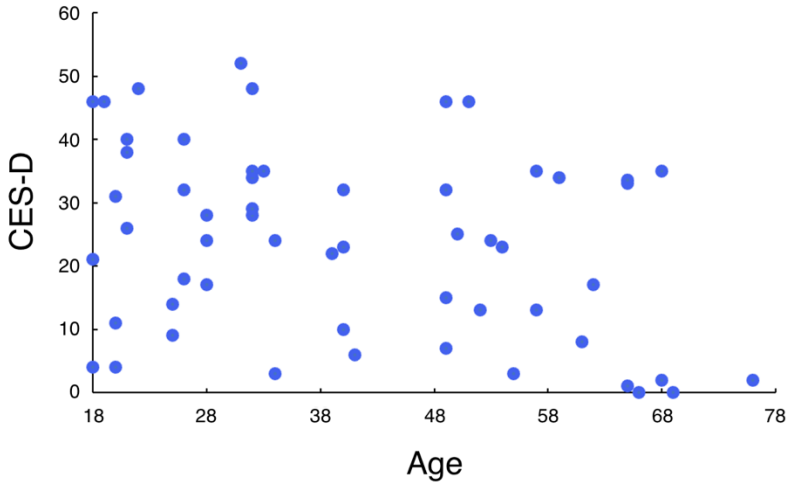

Figure 1 – Relationship Between Age and CES-D Score

2.2 Materials

2.2.1 Questionnaires and Neuropsychological Assessments

After completing consent, health, and fMRI screening forms, participants were administered a series of questionnaires and neuropsychological assessments. The 20-item Positive and Negative Affect Schedule Short Form (PANAS-SF; Watson et al., 1988) provided positive and negative affect scores based on participants' current mood state (completed before and after the scanning session). The Logical Memory subtests from the Wechsler Memory Scale (WMS-IV; Wechsler, 2009) assessed participants' immediate and delayed recall and recognition of two short stories read aloud by the experimenter. The Center for Epidemiological Studies Depression Scale Revised (CESD-R; Eaton et al., 2004) assessed depressive symptomology, with possible scores ranging from zero to 60.

The 21-item Depression, Anxiety, and Stress Scale (DASS-21; Lovibond & Lovibond, 1995) assessed symptoms of each, with possible scores ranging from zero to 42 for each subscale. The Emotion Regulation Questionnaire (ERQ; Gross & John, 2003) is a 10-item scale that measures use of cognitive reappraisal and expressive suppression strategies, with possible scores of 7-42 and 7-28, respectively. The Global Physical Activity Questionnaire (GPAQ; Armstrong & Bull, 2006) assessed occupational and recreational physical activity. The Mini-Mental State Exam (MMSE; Folstein et al., 1975) and Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005) were used to screen for possible mild cognitive impairment.

The CES-D was ultimately chosen over the DASS-21 Depression as the main measure of depressive symptoms for all analyses. This decision was made because the CES-D includes nearly three times as many questions (20 vs. 7) and each question maps onto a symptom of depression in the Diagnostic and Statistical Manual (DSM-5) used for diagnosis (American Psychiatric Association, 2013).

2.2.2 Stimuli

Stimuli consisted of 396 images from the Nencki Affective Picture System (NAPS; Marchewka et al., 2014) and International Affective Picture System (IAPS; Lang et al., 2008). Image selection began with negative images, which were selected to be the most unpleasant and arousing images based on published standardized norms using the Self-Assessment Manikin (SAM) scale (valence: 1 = very negative, 9 = very positive; arousal: 1 = relaxed, 9 = aroused). Positive images were selected to match the arousal ratings of the negative images. An equal number of positive ($M_{valence}$ = 7.10 ± 0.38, $M_{arousal}$ = 5.53 ±

0.56), neutral ($M_{valence}$ = 5.59 ± 0.42, $M_{arousal}$ = 4.09 ± 0.69), and negative ($M_{valence}$ = 3.57 ± 0.83, $M_{arousal}$ = 5.54 ± 0.38) images were used. Positive and negative images did not significantly differ in terms of arousal (p = .77), however both were significantly more arousing than neutral images (ps < .001). Three auditory cues were selected from the International Affective Digitized Sounds (IADS) system (Bradley & Lang, 2007). All cues were one second clips: the positive cue was a winning slot machine sound (sound #717; $M_{pleasure}$ = 7.32 ± 1.67, $M_{arousal}$ = 6.56 ± 2.19), the neutral cue was a whistling sound (sound #270; $M_{pleasure}$ = 6.10 ± 1.83, $M_{arousal}$ = 4.23 ± 2.06), and the negative cue was a screeching tires sound (sound #422; $M_{pleasure}$ = 2.22 ± 1.47, $M_{arousal}$ = 7.52 ± 1.90). All stimuli were presented using a custom PsychoPy (Peirce, 2007) program.

2.3 Design and Procedure

The study was divided into encoding (Figure 2 A) and retrieval (Figure 2 B) stages. fMRI data were collected only during encoding. Before beginning each stage of the experiment, participants were guided through instructions and practice trials outside of the scanner. Practice was repeated as necessary until clear understanding was demonstrated. Stimuli were counterbalanced across participants such that the 126 new images at retrieval differed across participants.

2.3.1 Encoding

The encoding stage was divided into four blocks, each with 84 trials. Each block consisted of 63 full trials and 21 catch trials. As illustrated in Figure 2 A, all trials started with the auditory cue that signaled the valence of the upcoming stimulus, followed by a

brief fixation period. For the full trials, the stimulus was then presented, and participants were tasked with rating the emotional intensity of the image on a 1-4 scale, with 1 being the least intense and 4 being the most intense. To make their intensity judgments, participants were given two MRI compatible response boxes and were asked to use their left middle finger to indicate "1", left index finger for "2", right index finger for "3", and right middle finger for "4". Following another brief fixation period, a series of arrows then appeared on the screen, and participants were asked to use the buttons on the appropriate box to indicate the direction the arrow was pointing. This "arrows task" maximizes design efficiency by pseudorandomly interspersing event trials with "active" baseline trials lasting between 1.5 and 4.5 seconds, jittered in increments of 1.5 seconds (Dale, 1999). Requiring participants to respond to the arrows ensured they remained engaged in the task, and default mode network activity was minimized (Stark & Squire, 2001). For the catch trials, no stimulus was shown; the arrows task began immediately after the fixation period following the cue. Catch trials were included to estimate unique cue-related activity, as has been done in previous studies (e.g., Corbett et al., 2020; Corbetta et al., 2000; Sussman et al., 2017; Wheeler et al., 2006).

After exiting the scanner, participants were asked to complete the PANAS-SF scale again to assess changes in mood state and a brief survey to identify any emotional regulation strategies they employed in response to positive, neutral, and negative stimuli. Specifically, the survey asked how often (always/sometimes/never) they closed or averted their eyes, reappraised the images to be either more or less emotional, distracted themselves, suppressed their emotional reaction, or focused on peripheral details of the image. Additionally, in an open-ended format, we asked what thoughts, feelings, or

physical reactions they had in response to each of the cue types. Once participants completed the survey, they began the retrieval task.

2.3.2 Retrieval

The retrieval stage was divided into six blocks, with 63 trials (42 old, 21 new) in each. As illustrated in Figure 2 B, participants first made a recognition decision to decide whether the image had been shown during encoding, then they rated their confidence in that decision on a 1-7 scale, where 1 meant not at all confident and 7 meant highest possible confidence. Confidence judgments were used to distinguish high confidence (5-7) trials from medium (4) and low confidence (1-3) trials.

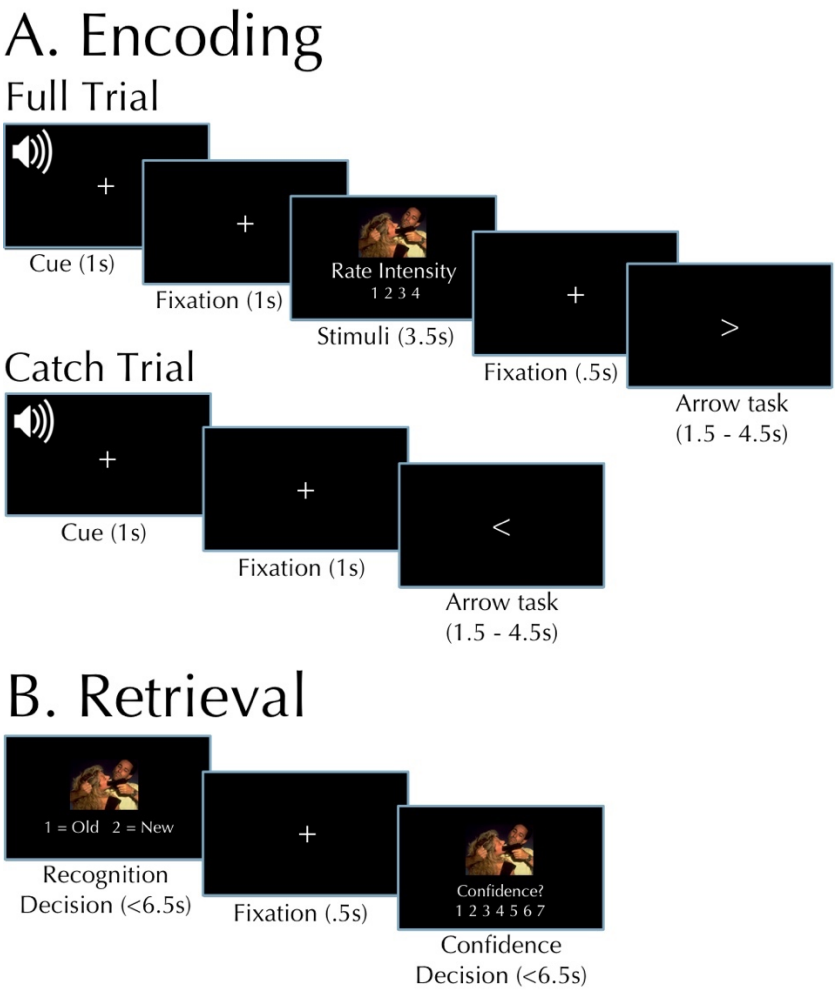

Figure 2 – Experimental Design

2.4 Behavioral Analyses

To investigate the relationship between age, depressive symptoms (measured by CES-D score), and data from the various questionnaires, these variables were entered into regression equations with age and CES-D as predictors and questionnaire scores as outcomes. The predictor variables were centered around their respective means.

Memory performance was estimated using the *Pr* discrimination index: p(hit) – p(false alarm) and memory bias was estimated using the *Br* bias index: p(false alarm)/(1 –

Pr) (Snodgrass & Corwin, 1988). Neutral bias is represented as $Br = 0.5$; liberal bias (i.e., tendency to say retrieval items are old) is represented as $Br > 0.5$; conservative bias (i.e., tendency to say retrieval items are new) is represented as $Br < 0.5$. *Pr* and *Br* were selected over *d′* and *c* because the value for *c* falls between -1 and 1. Many of the analyses assessed participants' performance on one valence category relative to their performance on another valence category; because I created difference scores (e.g., negative – neutral), having a bias index that can only be a positive value allows for a more precise estimate of liberal versus conservative bias.

To investigate the influence of age and depressive symptoms on behavioral measures (i.e., intensity ratings, response times, memory discriminability, and memory bias), I created positive – neutral, negative – neutral, and negative – positive difference scores. These values were entered into separate hierarchical regression equations as the outcome variable, with age and CES-D score entered as predictors in Model 1, and the interaction between these two variables was added in Model 2. The predictor variables were centered around their respective means. This method was followed in all analyses where unique and interactive effects of age and depressive symptoms were investigated as predictors. All analyses were conducted in SPSS Version 24. Regression analyses testing moderation effects (i.e., Age x CES-D interactions) were conducted using the PROCESS macro for SPSS (Hayes, 2012). ANOVA results for across-participant analyses were reported using Huynh-Feldt corrections, reflected in the reported degrees of freedom and *p* values, where appropriate.

2.5 fMRI Acquisition

Scanning was performed on a Siemens 3T MAGNETOM Prisma-Fit MRI system at the Center for Advanced Brain Imaging on the Georgia Institute of Technology campus. Functional data were acquired using a gradient-echo pulse sequence (38 transverse slices oriented along the anterior–posterior commissural axis with a 30° upward tilt to avoid the eyes, repetition time = 1155 msec, echo time = 30 msec, 3.4 x 3.4 x 3.4 mm voxels). Four encoding blocks of 586 volumes each were acquired. The first two volumes of each block were discarded to allow for equilibration effects. A high-resolution T1-weighted magnetization-prepared rapid acquisition gradient-echo (MPRAGE) image was collected for normalization.

2.6 fMRI Analysis

2.6.1 Region of Interest (ROI) Definition

Four bilateral ROIs were generated from the Anatomical Automatic Labeling (AAL) system (Tzourio-Mazoyer et al., 2002) implemented in the WFU Pickatlas toolbox (Maldjian et al., 2003)—amygdala, hippocampus, orbitofrontal cortex (OFC; consisting of superior, middle, inferior, and medial OFC AAL regions), and ventral occipitotemporal cortex (VOTC; consisting of fusiform, parahippocampal, inferior occipital, middle occipital, and inferior temporal AAL regions). For the PFC, I chose to use a functional ROI, as previous studies have reported involvement of regions that are not adequately captured by frontal AAL regions. One functional ROI was identified from a task > baseline univariate F contrast, using a familywise error correction ($p < .05$) and minimum threshold of 30 voxels. I selected a dmPFC cluster identified by the contrast (center at [0, 53, 29],

369 voxels), given the role of the medial PFC in emotional processing. The ROIs are shown in Figure 3.

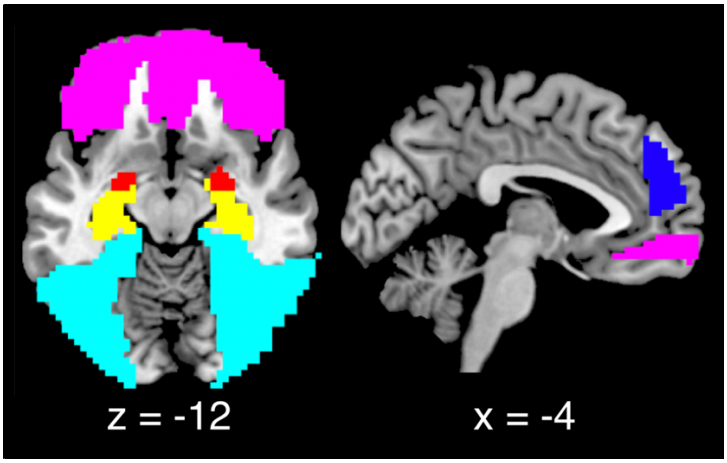

Figure 3 – ROIs Used in Imaging Analyses

Note. Red = amygdala, yellow = hippocampus, cyan = ventral occipitotemporal cortex (VOTC), blue = dmPFC, magenta = OFC.

2.6.2 Univariate Analysis

Data were analyzed with SPM12 (SPM12, www.fil.ion.ucl.ac.uk/spm/software/spm12/). Functional images were corrected for differences in slice timing acquisition using the middle slice of each volume as the reference, spatially realigned and resliced with respect to the first volume of the first block. Each participant's magnetization-prepared rapid acquisition gradient-echo scan was coregistered to the mean EPI image, produced from spatial realignment. Each coregistered structural scan was then be segmented using the Diffeomorphic Anatomical Registration Through Exponentiated Lie algebra (DARTEL) SPM12 toolbox (Ashburner, 2007). DARTEL is a suite of tools fully integrated with SPM12, which the SPM12 manual

recommends over optimized normalization to achieve sharper nonlinear registration, for intersubject alignment. This method also achieves better localization of fMRI activations in Montreal Neurological Institute (MNI) space and has been used successfully in several studies with healthy and neurological populations (Pereira et al., 2010; Yassa & Stark, 2009). Briefly, the gray and white matter segmented images were used to create a study-specific template using the DARTEL toolbox, and the flow fields containing the deformation parameters to this template for each subject were used to normalize each participant's realigned and resliced EPIs to MNI space. Normalized EPI images were written to 3 x 3 x 3 mm and smoothed with an 8-mm FWHM isotropic Gaussian kernel. The EPI data were then high-pass filtered to a minimum of 1/128 Hz and grand mean scaled to 100.

Neural activity was modeled to the onset of the stimulus (i.e., the image) as a series of 0 s epochs (i.e., delta functions) of the various event types (e.g., positive hits, negative hits) and convolved with a canonical hemodynamic response function. The time courses were then down-sampled to the middle slice to form the covariates for the general linear model (GLM). For each participant and block, six covariates representing residual movement-related artifacts, determined in the spatial realignment step, were included in the first level model to capture residual (linear) movement artifacts. Voxel-wise parameter estimates for these covariates were obtained by restricted maximum likelihood estimation, using a temporal high-pass filter (cutoff = 128 sec) to remove low-frequency drifts. Temporal autocorrelation across scans were modeled with an AR(1) process.

Contrasts of the parameter estimates for each participant were submitted to the second level model (treating participants as a random effect). A valence (positive, neutral,

negative) ANOVA model was created for the encoding period using only the full trials (i.e., no catch trials) in which participants provided intensity ratings (trials with no encoding response were excluded). Additionally, only subsequent hit trials ("Old" responses to previously studied images) were included in the ANOVA, as there were insufficient numbers[2] of misses ("New" responses to previously studied images) to examine subsequent memory effects (i.e., hit vs. miss). Covariates modeling the mean across conditions for each participant were also added to each model for all contrasts in the second-level model to remove between-subject variance of no interest, as per the optimal event-related fMRI suggestions in Chapter 10 of the SPM manual (SMP12; www.fil.ion.ucl.ac.uk/spm/doc/manual.pdf). I had planned to create an additional ANOVA model where emotional valence conditions were separated by intensity (e.g., positive high intensity hits, negative low intensity hits), however, several participants had too few trials for this analysis to be possible (three participants had < 10 positive low intensity hits, six had < 10 positive high intensity hits, and six had < 10 negative low intensity hits).

Region of interest (ROI) analyses were conducted for the regions defined above using the MarsBaR toolbox (http://marsbar.sourceforge.net/). Mean activity within each ROI was extracted for the three valence conditions for each participant. To determine whether activity in these regions differed as a function of valence across participants, I compared mean activity between positive, neutral, and negative conditions. To investigate whether age and depressive symptoms uniquely or interactively predicted encoding differences between valence conditions, I created positive – neutral, negative – neutral, and

[2] "Insufficient was defined as fewer than 10 trials per condition; 17 participants had < 10 positive misses, 15 had < 10 neutral misses, and 27 had < 10 negative misses.

negative – positive difference scores for each ROI to serve as the outcome variable. Hierarchical regressions were conducted as described above.

2.6.3 Representational Similarity Analysis

I used RSA to examine the similarity of activation patterns across full trials during encoding. Preprocessing of data for RSA was conducted in the same manner as that for the univariate analysis, with the exception of the normalization step. For RSA, normalized EPI images were smoothed with a 3-mm FWHM isotropic Gaussian kernel, as opposed to the 8mm Kernel used for univariate analyses. The first stage of analysis (i.e., the GLM) modeled neural activity to the onset of the cue. Residuals from the first level model (i.e., the pattern of activity not explained by the motion parameters) were saved and used for analyses. Patterns from each region of interest were extracted (spanning all trials with encoding and retrieval responses; catch trials and bad/no response trials were removed), and the residual maps were z-scored within voxels across time, separately within each run (removing run-level mean differences in the voxel activity level data). Because I was interested in activation patterns for stimulus processing, the first two TRs for each trial (overlapping in time with the cue and fixation period) were assigned a weight of zero while an average trial-wise activity pattern was generated from TRs 3-6 (equally weighted). Analyses were performed using an ROI approach with the five regions defined above.

Separately for each participant and each ROI, I computed neural similarity scores for negative, neutral, and positive valence categories. The neural similarity scores for each stimulus were calculated as the mean of the Pearson correlations between the event-specific weighted mean pattern corresponding to that stimulus and the event-specific weighted

mean pattern corresponding to the other stimuli either 1.) drawn from the same valence category (within-category similarity) or 2.) drawn from the neutral valence category (for positive and negative images) or from the emotional valence categories (for neutral images; between-category similarity) for each ROI. This yielded a within-category similarity score for each of the three valence categories and a between-category similarity score for each of the three valence categories (i.e., positive vs. neutral, negative vs. neutral, and neutral vs. emotional) for each participant and each ROI. Only subsequent hit trials were used for these comparisons. To determine whether each ROI has a unique way of representing valence categories, I created difference scores by subtracting between-category similarity from within-category similarity (negative with negative – negative with neutral, positive with positive – positive with neutral, and neutral with neutral – neutral with emotional; referred to as *negative category specific representations [CSR]*, *positive CSR*, and *neutral CSR*, respectively, from here out).

For each ROI, I first assessed whether CSR in each valence category significantly differed from zero; that is, whether within-valence category similarity was significantly greater than between-valence category similarity. Next, I analyzed whether CSR differed as a function of valence and ROI across participants. In the final across-participant analysis, I investigated whether CSR in each valence condition correlated with memory performance differences (e.g., negative CSR correlated with negative – neutral *Pr*). To investigate whether age and/or depressive symptoms affected unique pattern representations, separate hierarchical regressions were conducted using CSR for each valence condition as outcome variables; age and CES-D were entered as predictors in Model 1, and the interaction

between these variables was added in Model 2. The predictor variables were centered around their respective means.

2.6.4 Functional Connectivity Analysis

Data preprocessing was identical to that of univariate analyses. To determine if the anticipatory age-by-valence interactions in medial frontal-amygdala connectivity identified in a prior study (Corbett et al., 2020) replicated in the current study, I examined functional connectivity during catch trials using a vmPFC seed. The SPM12 generalized psychophysiological interactions (gPPI) toolbox (available at http://brainmap.wisc.edu/PPI) (McLaren et al., 2012) was used to estimate whole-brain connectivity with a 6mm volume of interest around the vmPFC voxel [18, 66, -3] that was identified in Corbett et al. (2020)'s behavioral partial least squares (PLS) analysis and used as the seed voxel in the seed PLS analysis. At the first level for each subject, the gPPI toolbox was used to (1) create psychological/task regressors, (2) create the physiological variable by estimating the BOLD signal observed in the vmPFC seed region, and (3) calculate the psychophysiological interaction terms by convolving the time course vectors with their corresponding valence condition vector. Three functional connectivity contrast images (one for each valence category compared to baseline) were created for each subject. At the second level, these contrast images were entered into random-effects analyses with age and CES-D scores included as continuous variables of interest. Parameter estimates of connectivity were then extracted from left and right amygdala AAL regions using marsbar. Age and depressive symptoms were examined as predictors of vmPFC-amygdala functional connectivity using hierarchical regression equations, with age and CES-D score entered in Model 1, and their interaction was added in Model 2. It should be noted that due

to signal dropout, three participants did not have data in the vmPFC sphere. The 53 participants with sufficient vmPFC data were used in this analysis.

A dmPFC seed was also identified from Corbett et al. (2020)'s behavioral PLS analysis (6mm volume of interest centered around [12, 60, 21]). The gPPI analysis using the dmPFC seed was conducted following the same steps outlined above. In addition to extracting parameter estimates of connectivity between the seed regions and amygdala, I also extracted estimates of connectivity between the seed regions and hippocampus and the VOTC ROIs defined above.

CHAPTER 3. RESULTS

3.1 Behavioral

3.1.1 Relationship Between Age, Depressive Symptoms, and Questionnaire Data

To investigate the relationship between age, depressive symptoms (measured by CES-D score), and data from the various questionnaires, these variables were entered into regression equations with age and CES-D as predictors and questionnaire scores as outcomes. The predictor variables were centered around their respective means. These results are presented in Table 1. Unsurprisingly, CES-D scores were positively associated with all three DASS-21 measures. Additionally, higher CES-D scores were associated with greater negative affect at baseline (PANAS), but not with baseline positive affect. Consistent with age-related decline in episodic memory, age was associated with worse performance across all three WMS Logical Memory measures.

Table 1 – Results for Regression Analyses with Age and CES-D Predicting Performance on Questionnaires

	B	*SE B*	*β*	R^2	*F* for R^2
DASS-21 Depression					
Age	0.064	0.056	.092	.683	57.019*
CES-D	0.674	0.065	.851*		
DASS-21 Anxiety					
Age	0.034	0.058	.063	.432	20.168*
CES-D	0.414	0.067	.675*		
DASS-21 Stress					
Age	-0.017	0.051	-.029	.623	43.879*
CES-D	0.517	0.059	.780*		
ERQ Reappraisal					
Age	0.099	0.061	.215	.177	5.718*
CES-D	-0.159	0.07	-.299*		
ERQ Suppression					

Age	0.017	0.046	.052	.066	1.869
CES-D	0.102	0.053	.269		
PANAS Positive at Baseline†					
Age	0.116	0.078	.208	.073	2.045
CES-D	-0.075	0.089	-.119		
PANAS Negative at Baseline†					
Age	-0.044	0.041	-.135	.249	8.623*
CES-D	0.163	0.047	.440*		
PANAS Positive Change†					
Age	0.037	0.058	.093	.011	0.301
CES-D	0.041	0.066	.090		
PANAS Negative Change†					
Age	0.013	0.034	.053	.066	1.839
CES-D	-0.064	0.039	-.235		
GPAQ Work-Related MET Minutes					
Age	24.08	19.304	.178	.031	0.848
CES-D	16.671	22.117	.108		
GPAQ Travel-Related MET Minutes					
Age	-1.474	11.54	-.019	.022	0.041
CES-D	2.669	13.222	.029		
GPAQ Leisure-Related MET Minutes					
Age	-9.903	12.39	-.115	.016	0.423
CES-D	-9.773	14.196	-.099		
WMS Logical Memory Immediate Recall††					
Age	-0.137	0.043	-.415*	.205	6.578*
CES-D	0.036	0.047	.100		
WMS Logical Memory Delayed Recall††					
Age	-0.203	0.064	-.421*	.180	5.596*
CES-D	0.006	0.07	.012		
WMS Logical Memory Recognition††					
Age	-0.056	0.021	-.362*	.136	3.998*
CES-D	0.003	0.023	.020		
MMSE					
Age	-0.007	0.006	-.145	.043	1.185
CES-D	0.006	0.007	.108		
MoCA					
Age	-0.066	0.020	-.441*	.179	5.772*
CES-D	-0.012	0.022	-.073		

*$p < .05$
†$n = 55$
††$n = 54$

3.1.2 Post-Scan Survey Data

3.1.2.1 Across Participants

The average frequency with which participants reported using the various emotion regulation strategies as measured in the post-scan survey is reported in Table 2. For analyses, responses were coded as follows: "never" = 0, "sometimes" = 1, "always" = 2. Using a Valence (positive, neutral, negative) ANOVA, I found that the average use of strategies varied as a function of valence, $F(2, 110) = 12.78$, $p < .001$, $\eta_p^2 = .19$; participants reported using strategies more often for negative than for positive or neutral images (ts > 2.89, ps < .005) and more often for neutral than for positive images ($t = 2.74$, $p = .008$).

Table 2 – Participants' Reported Use of Emotion Regulation Strategies During Encoding Task

Question	Response	Positive	Neutral	Negative
Closing your eyes?	Never	89.3	89.3	73.2
	Sometimes	10.7	10.7	25
	Always	0	0	1.8
Averting your eyes from the image?	Never	89.3	85.7	58.9
	Sometimes	10.7	14.3	37.5
	Always	0	3.6	3.6
Thinking of something unrelated to the image/task (i.e., distracting yourself)?	Never	51.8	44.6	48.2
	Sometimes	44.6	50	48.2
	Always	1.8 ††	5.4	3.6
Dampening your emotional reaction to the image?	Never	55.4	64.3	37.5
	Sometimes	42.9	35.7	53.6
	Always	1.8	0	8.9
Focusing on only peripheral (i.e., background) details of the image?	Never	67.9	66.1	51.8
	Sometimes	30.4	33.9	41.1
	Always	1.8	0	7.1
Reinterpreting the meaning of the image to be less emotional?	Never	53.6	—	30.4
	Sometimes	46.4	—	64.3
	Always	0	—	0 †
Reinterpreting the meaning of the image to be more positive?	Never	—	25	—
	Sometimes	—	73.2	—
	Always	—	1.8	—
Reinterpreting the meaning of the image to be more negative?	Never	—	41.1	—
	Sometimes	—	55.4	—
	Always	—	3.6	—

Note. The survey asked participants "When presented with a [insert valence] image, did you find yourself…". All values reported as percentages (%).

†3 participants (5.4%) did not provide responses to this question
††1 participant (1.8%) did not provide a response to this question

3.1.2.2 Effects of Age and Depressive Symptoms on Post-Scan Survey Data

To investigate whether age and depressive symptoms influenced differences in reported use of emotion regulation strategies between valence conditions, these variables were entered into regression equations with age and CES-D as predictors and difference scores between valence conditions as outcomes. The predictor variables were centered around their respective means. These results are presented in Table 3. No effects were significant.

Table 3 – Results for Regression Analyses with Age and CES-D Predicting Reported Use of Emotion Regulation Strategies During Encoding Task

	B	*SE B*	*β*	R^2	*F* for R^2
		Positive – Neutral			
Age	-0.002	0.002	-.147	.063	1.79
CES-D	0.003	0.002	.162		
		Negative – Neutral			
Age	-0.001	0.003	-.062	.004	0.10
CES-D	0	0.003	-.007		
		Negative – Positive			
Age	0.001	0.003	.048	.019	0.53
CES-D	-0.003	0.004	-.117		

*$p < .05$

3.1.3 Intensity Ratings and Response Times Across Participants

Across participants, intensity ratings differed between valence categories, $F(2, 108^{3}) = 109.57$, $p < .001$, $\eta_p^2 = .67$. Intensity ratings were highest for negative stimuli and lowest for neutral stimuli (negative vs. positive: $t(54) = 4.13$, $p < .001$; negative vs. neutral: $t(54) = 12.89$, $p < .001$; positive vs. neutral: $t(54) = 11.74$, $p < .001$). Intensity rating response times also differed as a function of valence, $F(2, 108) = 25.09$, $p < .001$, $\eta_p^2 = .32$. Responses were fastest for neutral stimuli and slowest for negative stimuli (negative vs. positive: $t(54) = 5.00$, $p = .01$; negative vs. neutral: $t(54) = 6.50$, $p < .001$; positive vs. neutral: $t(54) = 2.66$, $p < .001$). Means and standard deviations are presented in Table 4.

Table 4 – Intensity Responses and Memory Performance Across Participants

	Positive	Neutral	Negative
Intensity Rating	2.43 (0.55)	1.83 (0.49)	2.67 (0.47)
Response Time	1.62 (0.36)	1.57 (0.36)	1.69 (0.37)
Hits	.753 (.159)	.752 (.169)	.807 (.148)
False Alarms	.161 (.150)	.163 (.145)	.157 (.171)
Pr	.592 (.227)	.589 (.226)	.650 (.248)
High Intensity *Pr*	.607 (.276)	—	.670 (.242)
Low Intensity *Pr*	.576 (.226)	—	.609 (.276)
High Confidence *Pr*	.618 (.294)	.616 (.280)	.678 (.291)
Low + Medium Confidence *Pr*	.141 (.281)	.160 (.284)	.140 (.291)
Br	.387 (.215)	.403 (.243)	.424 (.237)
High Intensity *Br*	.406 (.215)	—	.451 (.248)
Low Intensity *Br*	.389 (.237)	—	.397 (.241)
High Confidence *Br*	.461 (.294)	.473 (.310)	.512 (.311)
Low + Medium Confidence *Br*	.343 (.185)	.350 (.189)	.366 (.189)

Note. Entries are in the format: mean (SD).

3.1.4 Memory Performance Across Participants

[3] One participant appeared to have rated valence instead of intensity, as their intensity ratings were highest for positive stimuli and lowest for negative stimuli; this individual was therefore removed from any analyses that involved intensity ratings

Table 4 presents the mean memory discriminability and bias estimates. Across participants, memory discriminability differed as a function of valence, $F(1.81, 99.58) = 13.24$, $p < .001$, $\eta_p^2 = .19$. Memory discriminability was higher for negative than for positive and neutral stimuli (ts > 4.07. ps < .001), but positive and neutral did not differ ($t = 0.285$, $p = .777$). Memory bias did not differ between valence categories, $F(2, 110) = 1.37$, $p = .259$, $\eta_p^2 = .02$).

To examine whether memory discriminability and bias were affected by intensity, Valence (positive, negative[4]) x Intensity (low, high) ANOVAs were conducted. For discriminability, the ANOVA revealed main effects of valence, $F(1, 54) = 8.70$, $p = .005$, $\eta_p^2 = .14$; and intensity, $F(1, 54) = 13.99$, $p < .001$, $\eta_p^2 = .21$; but no significant interaction, $F(1, 54) = 2.47$, $p = .122$, $\eta_p^2 = .04$. For bias, the main effect of intensity was significant, $F(1, 54) = 4.13$, $p = .047$, $\eta_p^2 = .07$; but valence, $F(1, 54) = 1.64$, $p = .206$, $\eta_p^2 = .03$; and the interaction, $F(1, 54) = 2.65$, $p = .110$, $\eta_p^2 = .05$, were not. As noted in the Method, imaging analyses were conducted for valence conditions collapsed across intensity ratings, as several participants had too few trials to split by intensity.

Finally, to explore whether memory discriminability and bias were affected by confidence, Valence (positive, neutral, negative) x Confidence (low/medium, high) ANOVAs were conducted. For discriminability, the ANOVA revealed only a main effect of confidence, $F(1, 55) = 154.38$, $p < .001$, $\eta_p^2 = .74$; neither the main effect of valence, $F(2, 110) = 1.08$, $p = .345$, $\eta_p^2 = .02$; nor the interaction was significant, $F(2, 110) = 2.06$,

[4] High and low intensity neutral trials were not defined for this analysis, as neutral images inherently are not highly arousing, and therefore participants only rarely rated them as such.

p = .132, η_p^2 = .04. Similarly, the ANOVA for bias revealed only a main effect of confidence, $F(1, 55) = 7.01$, p = .011, η_p^2 = .11; neither the main effect of valence, $F(2, 110) = 3.03$, p = .052, η_p^2 = .05; nor the interaction was significant, $F(2, 110) = 0.42$, p = .656, η_p^2 = .01. It should be noted that a majority of participants had too few low/medium confidence trials for these to be examined in subsequent analyses. Furthermore, a number of participants did not appear to use the confidence ratings as intended, given that their infrequent use of the low/medium confidence response was not related to high memory performance. Thus, the remainder of the results are presented collapsed across confidence.

3.1.5 Influence of Age and Depressive Symptoms on Intensity Ratings and RTs

Older age was negatively associated with negative – neutral intensity ratings. That is, older participants tended to provide lower intensity ratings for negative images relative to neutral images. All other relationships between predictors and outcomes were non-significant (see Table 5).

Table 5 – Results for Regression Analyses with Age and CES-D Predicting Intensity and RT

	Model 1			Model 2		
	B	*SE B*	*β*	*B*	*SE B*	*β*
Positive Intensity – Neutral Intensity						
Age	-0.006	0.003	-.259	-0.005	0.003	-.246
CES-D	-0.006	0.004	-.247	-0.006	0.004	-.247
Age x CES-D	—	—	—	0.0001	0	.064
R^2		.088			.092	
F for ΔR^2		2.502			0.22	
Negative Intensity – Neutral Intensity						
Age	-0.008	0.004	-.287*	-0.007	0.004	-.240
CES-D	-0.006	0.005	-.199	-0.006	0.004	-.200
Age x CES-D	—	—	—	0	0	.229
R^2		.086			.136	
F for ΔR^2		2.446			2.957	

Negative Intensity – Positive Intensity						
Age	-0.002	0.004	-.094	-0.001	0.004	-.052
CES-D	0	0.004	-.006	0	0.004	-.007
Age x CES-D	—	—	—	0	0	.200
R^2		.008			.047	
F for ΔR^2		0.223			2.046	
Positive RT – Neutral RT						
Age	0	0.001	-.021	0	0.001	-.019
CES-D	0	0.001	.029	0	0.001	.029
Age x CES-D	—	—	—	0.000004	0	.008
R^2		.002			.002	
F for ΔR^2		0.043			0.003	
Negative RT – Neutral RT						
Age	-0.001	0.001	-.167	-0.001	0.001	-.160
CES-D	0	0.001	.027	0	0.001	.027
Age x CES-D	—	—	—	0.00002	0	.034
R^2		.031			.032	
F for ΔR^2		0.842			0.057	
Negative RT – Positive RT						
Age	-0.001	0.001	-.187	-0.001	0.001	-.180
CES-D	-0.00001	0.001	-.001	-0.00001	0.001	-.001
Age x CES-D	—	—	—	0.00001	0	.033
R^2		.035			.036	
F for ΔR^2		0.942			0.056	

*$p < .05$

3.1.6 Influence of Age and Depressive Symptoms on Memory

Age significantly moderated the relationship between depressive symptoms and negative memory discriminability (i.e., negative *Pr* – neutral *Pr*; see Table 6). No significant effects were found for any of the bias analyses. Figure 4 presents the simple slopes for visualization of the moderator effect. Because the age moderation was significant, I also investigated whether this was the case for high and low intensity trials. This analysis revealed the moderator effect was significant only for high intensity negative memory discriminability ($p = .020$; low intensity: $p = .128$).

Table 6 – Results for Regression Analyses with Age and CES-D Predicting Memory Performance

	Model 1			Model 2		
	B	*SE B*	*β*	*B*	*SE B*	*β*
			Positive *Pr* – Neutral *Pr*			
Age	-0.00008	0.001	-.016	0	0.001	.041
CES-D	0	0.001	.034	0	0.001	.029
Age x CES-D	—	—	—	0.00008	0	.269
R^2		.002			.071	
F for ΔR^2		0.047			3.856	
			Negative *Pr* – Neutral *Pr*			
Age	0.00001	0.001	.002	0	0.001	.073
CES-D	0	0.001	.024	0	0.001	.018
Age x CES-D	—	—	—	0	0	.333*
R^2		.001			.106	
F for ΔR^2		0.015			6.146*	
			Negative *Pr* – Positive *Pr*			
Age	0.00009	0.001	.014	0	0.001	.045
CES-D	-0.000002	0.001	0	-.00002	0.001	-.003
Age x CES-D	—	—	—	.00006	0	.146
R^2		0			.021	
F for ΔR^2		0.005			1.082	
			Positive *Br* – Neutral *Br*			
Age	0.002	0.001	.229	0.002	0.001	.232
CES-D	0.001	0.001	.142	0.001	0.001	.142
Age x CES-D	—	—	—	0.000006	0	.011
R^2		.052			.052	
F for ΔR^2		1.448			0.006	
			Negative *Br* – Neutral *Br*			
Age	0	0.001	-.048	-0.001	0.001	-.064
CES-D	0	0.002	.038	0	0.002	.040
Age x CES-D	—	—	—	-0.00005	0	-.074
R^2		.005			.01	
F for ΔR^2		0.133			0.276	
			Negative *Br* – Positive *Br*			
Age	-0.003	0.001	-.245	-0.003	0.002	-.261
CES-D	-0.001	0.002	-.087	-0.001	0.002	-.086
Age x CES-D	—	—	—	-0.00005	0	-.079
R^2		.054			.06	
F for ΔR^2		1.505			0.328	

*$p < .05$

As can be seen in Figure 4, at the mean age of the sample, CES-D score did not have much of an effect on memory differences between negative and neutral images. However, at older ages (one standard deviation above the mean), higher CES-D score was associated with larger memory performance differences between negative and neutral images. Younger individuals (one standard deviation below the mean) tended to show the opposite trend: lower CES-D score was associated with larger memory performance differences between negative and neutral images.

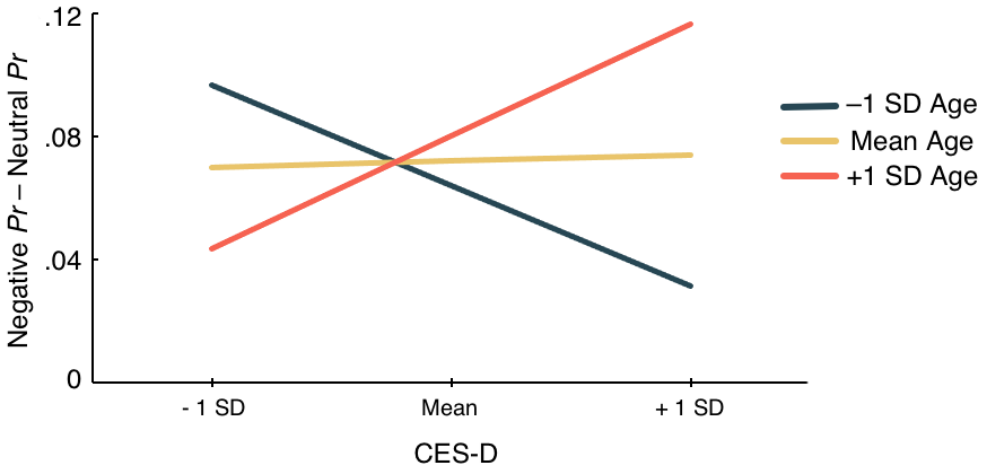

Figure 4 – Simple Slopes for Age and CES-D Predicting Negative Memory Discriminability.

Note. The *p* value for the interaction term: $p = .016$.

3.2 Imaging

3.2.1 Univariate

3.2.1.1 Across Participants

Figure 5 shows the mean activity differences between positive, neutral, and negative subsequent hit trials. To determine whether activity differed across valence conditions or ROIs, I conducted a Valence (positive, neutral, negative) x ROI (amygdala, hippocampus, VOTC, dmPFC, OFC) ANOVA. This revealed main effects of Valence, $F(2, 110) = 29.48$, $p < .001$, $\eta_p^2 = .35$; and ROI, $F(1.63, 89.87) = 230.32$, $p < .001$, $\eta_p^2 = .81$; as well as a significant interaction, $F(5.09, 279.71) = 20.23$, $p < .001$, $\eta_p^2 = .27$. To identify the source of the interaction, separate ANOVAs were conducted to compare valence within each ROI. The main effect of valence was significant in each ANOVA, Fs > 7.39, ps < .001, η_p^2s > .12, except in the hippocampus, $F(2, 110) = 0.81$ 7.39, $p = .446$, $\eta_p^2 = .02$. OFC did not distinguish between positive and neutral trials ($t = 1.59$, $p = .118$), but did distinguish between negative and neutral trials ($t = 3.57$, $p = .001$); the comparison between negative and positive did not survive Bonferroni corrections ($t = 2.44$, $p = .018$). Amygdala activity was greater for negative than neutral trials ($t = 4.05$, $p < .001$); comparisons between positive and neutral ($t = 2.33$, $p = .024$) and positive and negative ($t = 2.38$, $p = .021$) did not survive corrections. Within dmPFC and VOTC, activity was greater for negative trials than for positive (ts > 2.65, ps < .010) and neutral trials (ts > 6.94, ps < .001), and greater for positive trials than for neutral trials (ts > 2.69, ps < .010).

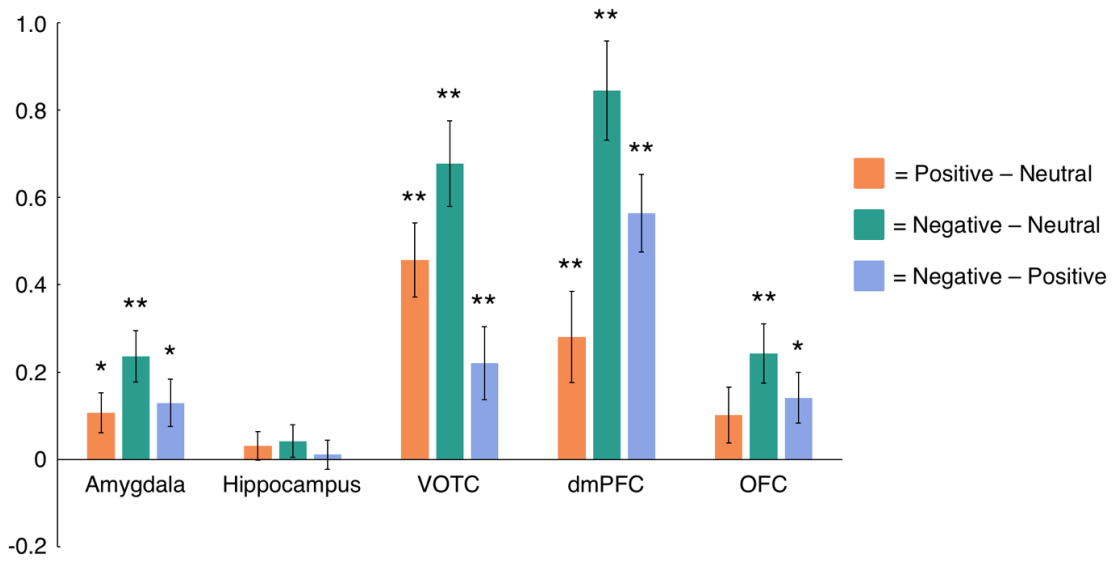

Figure 5 – Mean Univariate Activity Differences Between Valence Conditions Across Participants

Note. VOTC = ventral occipital temporal cortex, dmPFC = dorsomedial prefrontal cortex, OFC = orbitofrontal cortex. Asterisks indicate whether activity in the two conditions represented in each bar significantly differed. Error bars represent the standard error of the mean.

*$p < .05$
**$p < .0167$ (Bonferroni correction threshold)

3.2.1.2 Relationship Between Univariate Activity and Memory Across Participants

Only correlations between negative – positive BOLD activity and negative – positive *Pr* emerged as significant. Within both the hippocampus ($r = -.271$, $p = .043$) and VOTC ($r = -.318$, $p = .017$), negative – positive activity predicted worse negative relative to positive memory discriminability. All other correlations between activity and memory discriminability and bias were non-significant ($rs < .233$, $ps > .083$).

3.2.1.3 Influence of Age and Depressive Symptoms on Univariate Activity

Higher CES-D score was associated with lower amygdala activity for emotional (both positive and negative) relative to neutral trials, while older age was associated with lower amygdala activity only for negative – neutral trials (see Table 7). Within the VOTC, age significantly moderated the relationship between CES-D and positive – neutral activity. The simple slopes for this moderator effect are shown in Figure 6. At low levels of depression (-1 SD CES-D), older participants (+1 SD age) showed greater VOTC activity for positive than neutral trials than did younger participants (-1 SD age). With increasing levels of depression, older participants (+1 SD age) showed a reduction in positive VOTC activity, while younger participants (-1 SD age) showed a slight increase.

Table 7 – Results for Regression Analyses with Age and CES-D Predicting Univariate Activity Valence Differences

	Model 1			Model 2		
	B	*SE B*	*β*	*B*	*SE B*	*β*
Amygdala						
Positive – Neutral						
Age	-0.003	0.003	-.172	-0.003	0.003	-.185
CES-D	-0.008	0.003	-.344*	-0.008	0.003	-.343*
Age x CES-D	—	—	—	-0.00008	0	-.062
R^2		.110			.114	
F for ΔR^2		3.275*			0.212	
Negative – Neutral						
Age	-0.01	0.003	-.395*	-0.011	0.003	-.415*
CES-D	-0.009	0.004	-.307*	-0.009	0.004	-.305*
Age x CES-D	—	—	—	0	0	-.092
R^2		.173			.181	
F for ΔR^2		5.529*			0.512	
Negative – Positive						
Age	-0.007	0.003	-.279	-0.007	0.003	-.289
CES-D	-0.001	0.004	-.039	-0.001	0.004	-.038
Age x CES-D	—	—	—	-0.00007	0	-.047
R^2		.072			.074	
F for ΔR^2		2.067			0.117	

Hippocampus						
		Positive – Neutral				
Age	-0.001	0.002	-.051	-0.001	0.002	-.088
CES-D	-0.003	0.002	-.198	-0.003	0.002	-.194
Age x CES-D	—	—	—	0	0	-.174
R^2		.035			.064	
F for ΔR^2		0.968			1.602	
		Negative – Neutral				
Age	-0.003	0.002	-.186	-0.003	0.002	-.189
CES-D	-0.003	0.003	-.185	-0.003	0.003	-.185
Age x CES-D	—	—	—	-0.00001	0	-.014
R^2		.047			.047	
F for ΔR^2		1.301			0.01	
		Negative – Positive				
Age	-0.002	0.002	-.156	-0.002	0.002	-.123
CES-D	0	0.002	-.011	0	0.002	-.014
Age x CES-D	—	—	—	0	0	.155
R^2		.023			.046	
F for ΔR^2		0.637			1.245	
VOTC						
		Positive – Neutral				
Age	-0.00004	0.005	.001	-0.002	0.005	-.058
CES-D	-0.006	0.006	-.139	-0.006	0.006	-.133
Age x CES-D	—	—	—	-0.001	0	-.278*
R^2		.019			.093	
F for ΔR^2		0.523			4.215*	
		Negative – Neutral				
Age	-0.002	0.006	-.048	-0.004	0.006	-.087
CES-D	0.001	0.007	.021	0.001	0.007	.025
Age x CES-D	—	—	—	-0.001	0	-.186
R^2		.003			.036	
F for ΔR^2		0.089			1.785	
		Negative – Positive				
Age	-0.002	0.005	-.057	-0.002	0.005	-.043
CES-D	0.007	0.006	.167	0.007	0.006	.165
Age x CES-D	—	—	—	0	0	.065
R^2		.037			.041	
F for ΔR^2		1.021			0.221	
dmPFC						
		Positive – Neutral				
Age	-0.006	0.007	-.128	-0.006	0.007	-.125
CES-D	-0.006	0.008	-.122	-0.006	0.008	-.123
Age x CES-D	—	—	—	0.00004	0	0.015
R^2		.021			.022	
F for ΔR^2		0.578			0.011	
		Negative – Neutral				

Age	-0.012	0.007	-.246	-0.014	0.007	-.281
CES-D	0.001	0.008	.013	0.001	0.008	.016
Age x CES-D	—	—	—	-0.001	0	-.162
R^2		.063			.088	
F for ΔR^2		1.778			1.429	
			Negative – Positive			
Age	-0.006	0.005	-.166	-0.008	0.005	-.214
CES-D	0.007	0.006	.161	0.007	0.006	.165
Age x CES-D	—	—	—	-0.001	0	-.226
R^2		.071			.120	
F for ΔR^2		2.017			2.882	
			OFC			
			Positive – Neutral			
Age	0.002	0.004	.067	0.001	0.004	.049
CES-D	-0.007	0.005	-.205	-0.007	0.005	-.203
Age x CES-D	—	—	—	0	0	-.086
R^2		.055			.062	
F for ΔR^2		1.55			0.39	
			Negative – Neutral			
Age	-0.001	0.004	-.048	-0.002	0.004	-.053
CES-D	-0.003	0.005	-.094	-0.003	0.005	-.093
Age x CES-D	—	—	—	-0.00004	0	-.023
R^2		.008			.009	
F for ΔR^2		0.219			0.027	
			Negative – Positive			
Age	-0.003	0.004	-.130	-0.003	0.004	-.115
CES-D	0.003	0.004	.116	0.003	0.004	.115
Age x CES-D	—	—	—	0	0	.068
R^2		.040			.044	
F for ΔR^2		1.106			0.237	

*$p < .05$

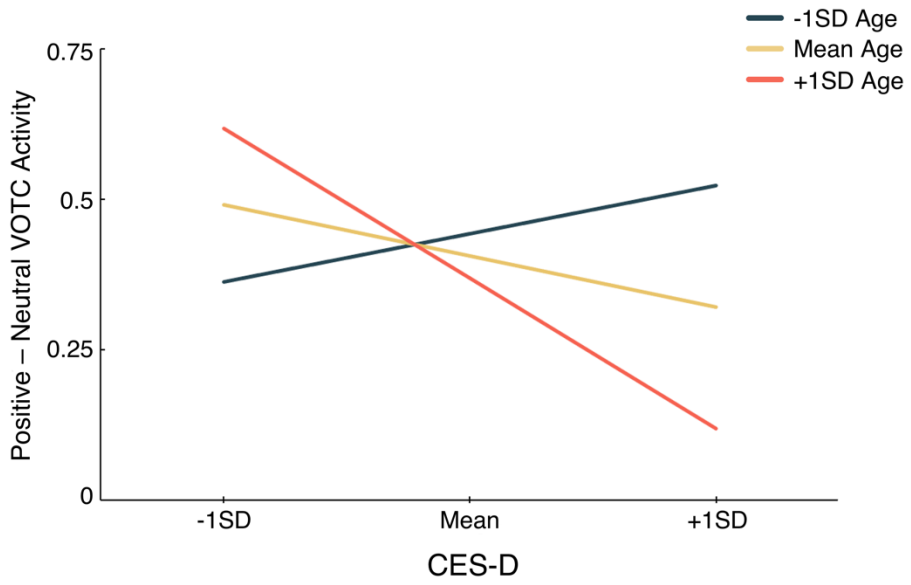

Figure 6 – Simple Slopes for Age and CES-D Predicting VOTC Positive – Neutral Activity

3.2.2 Representational Similarity Analysis

3.2.2.1 Across Participants

Across age and depression, positive CSR was significantly greater than zero (meaning within-valence category similarity was significantly greater than between-valence category similarity) in all ROIs (*t*s > 2.95, *p*s < .005) except the amygdala ($t = 1.82$, $p = .075$). Neutral CSR was not significantly greater than zero in any ROI (*t*s < 1.00, *p*s > .322) except the dmPFC, however this comparison did not survive Bonferroni corrections ($t = 2.05$, $p = .045$). Negative CSR was significantly greater than zero in all ROIs (*t*s > 4.30, *p*s < .001). Figure 7 shows these CSR estimates.

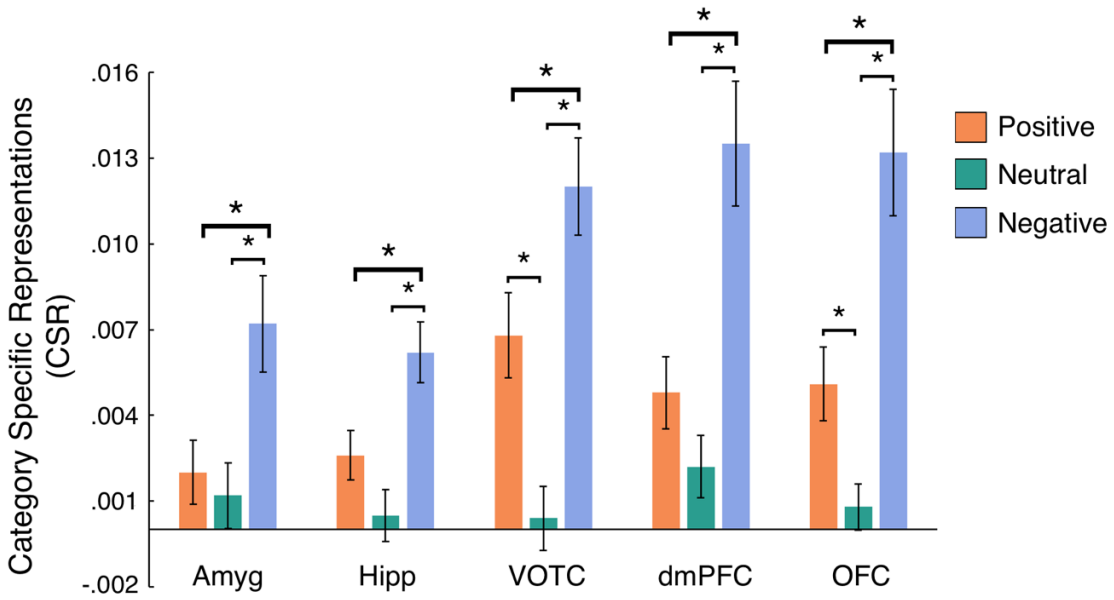

Figure 7 – Mean CSR Across Participants

Note. Amyg = amygdala, Hipp = hippocampus, VOTC = ventral occipitotemporal cortex, dmPFC = dorsomedial prefrontal cortex, OFC = orbitofrontal cortex. *$p < .05$.

To determine whether CSR differed as a function of valence or ROI, I conducted a Valence (positive, neutral, negative) x ROI (amygdala, hippocampus, VOTC, dmPFC, OFC) ANOVA. The ANOVA revealed main effects of Valence, $F(1.85, 101.63) = 7.03$, $p = .002$, $\eta_p^2 = .113$; and ROI, $F(3.46, 190.31) = 2.93$, $p = .028$, $\eta_p^2 = .051$; as well as a significant interaction, $F(3.92, 215.75) = 17.56$, $p < .001$, $\eta_p^2 = .242$. To identify the source of the interaction, separate ANOVAs were conducted to compare valence within each ROI. The main effect of valence was significant in each ANOVA, Fs > 7.17, ps < .001, η_p^2s > .115. Within both VOTC and OFC, positive CSR was significantly greater than neutral CSR (ts > 2.87, ps < .006); positive and neutral CSR did not differ within the other ROIs

(ts < 1.58, ps < .120). Within all ROIs, negative CSR was significantly greater than both positive (ts > 2.94, ps < .005) and neutral CSR (ts > 3.19, ps < .002).

3.2.2.2 Relationship Between CSR and Memory Across Participants

I investigated whether CSR for each valence condition in each ROI correlated with differences in *Pr* and *Br* between valence conditions (negative – neutral, positive – neutral, and negative – positive), however, none of the correlations were significant (rs < .24, ps > .079).

3.2.2.3 Influence of Age and Depressive Symptoms on CSR

To determine whether age and/or depressive symptoms affected CSR for positive, neutral, and negative trials, I conducted hierarchical regression analyses. Table 8 presents the results of these analyses. Age predicted lower positive CSR in the amygdala, hippocampus, and OFC; lower negative CSR in the amygdala, hippocampus, and dmPFC; and lower neutral CSR in the amygdala and OFC. CES-D predicted lower positive CSR in the amygdala. Additionally, age significantly moderated the relationship between CES-D and positive CSR in the OFC. The simple slopes for this interaction are shown in Figure 8. Individuals with low depressive symptoms (-1 SD CES-D) showed positive CSR values that were similar across age. However, with increasing depressive symptoms, younger participants (-1 SD age) showed an increase in positive CSR while older participants (+1 SD age) showed a decrease.

Table 8 – Results for Regression Analyses with Age and CES-D Predicting CSR

	Model 1			Model 2		
	B	*SE B*	*β*	*B*	*SE B*	*β*

Amygdala						
		Positive CSR				
Age	0	0	-.293*	0	0	-.294*
CES-D	0	0	-.308*	0	0	-.308*
Age x CES-D	—	—	—	-0.0000002	0	-.006
R^2		.123			.123	
F for ΔR^2		3.709*			0.002	
		Neutral CSR				
Age	0	0	-.363*	0	0	-.352*
CES-D	-0.0001	0	-.106	-0.0001	0	-.107
Age x CES-D	—	—	—	0.000002	0	.053
R^2		.119			.121	
F for ΔR^2		3.566*			0.157	
		Negative CSR				
Age	0	0	-.289*	0	0	-.261
CES-D	-0.00003	0	-.038	-0.00003	0	-.040
Age x CES-D	—	—	—	0.00001	0	.132
R^2		.078			.094	
F for ΔR^2		2.233			0.947	
Hippocampus						
		Positive CSR				
Age	0	0	-.268	0	0	-.296*
CES-D	0.00001	0	.024	0.00001	0	.026
Age x CES-D	—	—	—	-0.000003	0	-.131
R^2		.076			.093	
F for ΔR^2		2.190			0.937	
		Neutral CSR				
Age	0.00003	0	.067	0.00003	0	.080
CES-D	-0.00003	0	-.058	-0.00003	0	-.059
Age x CES-D	—	—	—	0.000001	0	.059
R^2		.010			.014	
F for ΔR^2		0.278			0.176	
		Negative CSR				
Age	0	0	-.306*	0	0	-.329*
CES-D	-0.00002	0	-.030	-0.00002	0	-.028
Age x CES-D	—	—	—	-0.000003	0	-.111
R^2		.088			.100	
F for ΔR^2		2.572			0.680	
VOTC						
		Positive CSR				
Age	0	0	-.167	0	0	-.157
CES-D	0.0001	0	.095	0.0001	0	.094
Age x CES-D	—	—	—	0.000002	0	.045
R^2		.047			.049	
F for ΔR^2		1.303			0.103	

		Neutral CSR				
Age	-0.0001	0	-.107	-0.00005	0	-.100
CES-D	0.00001	0	.025	0.00001	0	.024
Age x CES-D	—	—	—	0.000001	0	.035
R^2		.014			.015	
F for ΔR^2		0.372			0.060	
		Negative CSR				
Age	0	0	-.154	0	0	-.193
CES-D	0	0	.230	0	0	.233
Age x CES-D	—	—	—	-0.00001	0	-.180
R^2		.099			.130	
F for ΔR^2		2.920			1.837	
		dmPFC				
		Positive CSR				
Age	-0.0001	0	-.145	-0.0001	0	-.133
CES-D	-0.0001	0	-.095	-0.0001	0	-.097
Age x CES-D	—	—	—	0.000002	0	.056
R^2		.021			.024	
F for ΔR^2		0.578			0.160	
		Neutral CSR				
Age	-0.0001	0	-.153	-0.0001	0	-.190
CES-D	0.0001	0	.121	0.0001	0	.125
Age x CES-D	—	—	—	-0.00001	0	-.175
R^2		.050			.079	
F for ΔR^2		1.391			1.644	
		Negative CSR				
Age	0	0	-.328*	0	0	-.370*
CES-D	0	0	.145	0	0	.149
Age x CES-D	—	—	—	-0.00001	0	-.197
R^2		.159			.196	
F for ΔR^2		5.024*			2.378	
		OFC				
		Positive CSR				
Age	0	0	-.253	0	0	-.311*
CES-D	-0.00002	0	-.024	-0.00001	0	-.018
Age x CES-D	—	—	—	-0.00001	0	-.273*
R^2		.061			.132	
F for ΔR^2		1.708			4.263*	
		Neutral CSR				
Age	0	0	-.369*	0	0	-.342*
CES-D	0.00001	0	.017	0.00001	0	.014
Age x CES-D	—	—	—	0.000003	0	.126
R^2		.140			.155	
F for ΔR^2		4.320*			0.934	
		Negative CSR				
Age	0	0	-.241	0	0	-.280

CES-D	0.00002	0	.014	0.00002	0	.018
Age x CES-D	—	—	—	-0.00001	0	-.184
R^2		.060			.093	
F for ΔR^2		1.701			1.852	

*$p < .05$

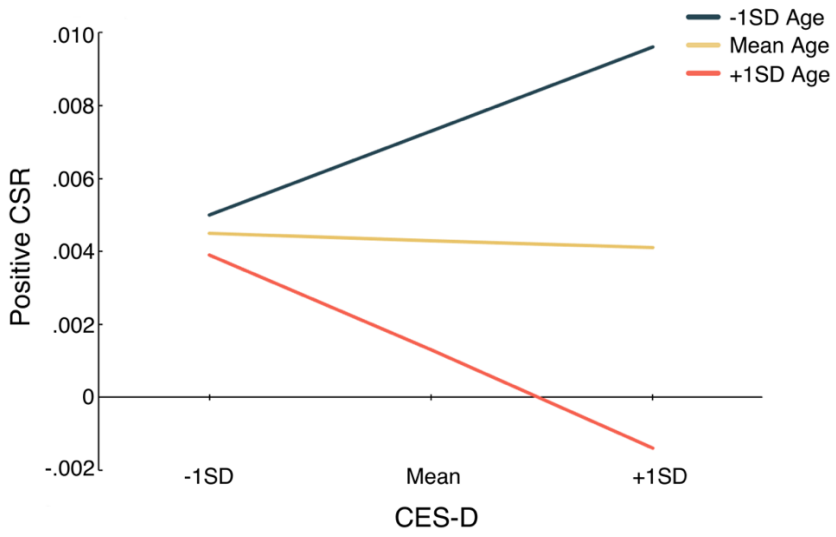

Figure 8 – Simple Slopes for Positive CSR in OFC

To determine whether the trends with age and CES-D were more a function of within- or between-valence category similarity, age and CES-D were separately split into tertials to explore the significant effects reported in Table 8. The mean within- and between-valence category similarity scores are presented for the youngest third (n = 19, mean age = 22.63, SD = 3.64) and oldest third (n = 19, mean age = 60.68, SD = 7.25) of participants in Figure 9. Between-valence category similarity did not differ between the youngest and oldest participants in any valence condition in any ROI ($ts < 1.93$, $ps > .062$). Within-valence category similarity was greater for the youngest participants than the oldest participants for neutral valence in the amygdala and OFC ($ts > 2.82$, $ps < .008$), for negative valence in the dmPFC and OFC ($ts > 2.31$, $ps < .027$), and for positive valence in the

hippocampus (t = 2.81, p = .008), however these comparisons did not survive Bonferroni corrections. The two groups did not differ on within-valence category similarity for positive or negative valence in the amygdala or negative valence in the hippocampus (ts < 1.44, ps > .159).

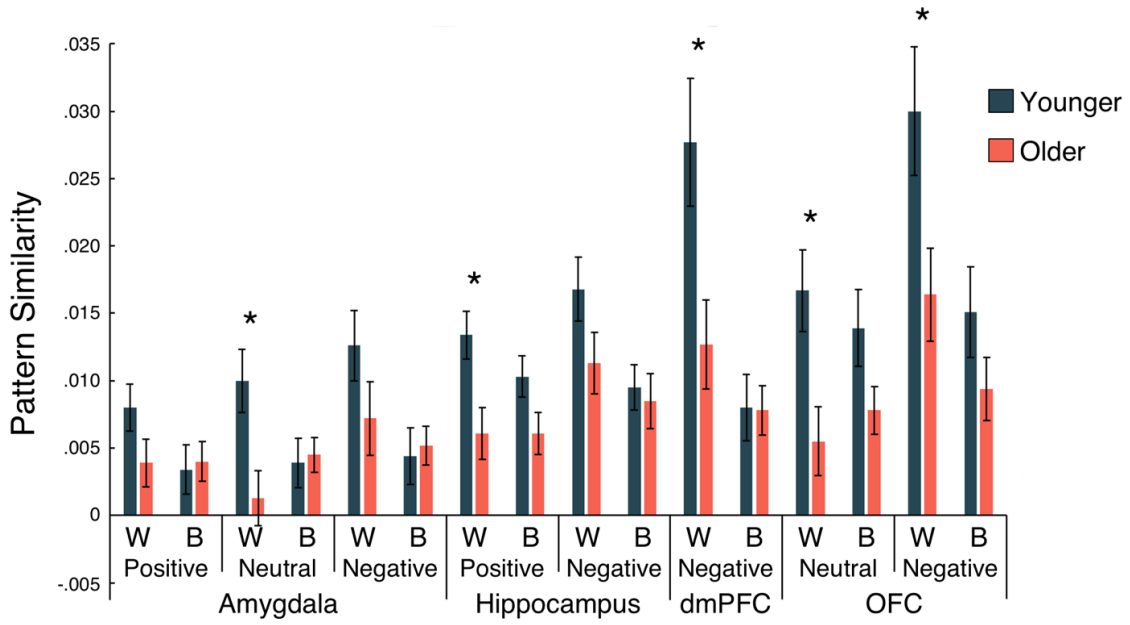

Figure 9 – Within- and Between-Valence Category Similarity for the Youngest and Oldest Participants

Note. W = within-valence category similarity, B = between-valence category similarity, Younger = the youngest third of the sample, Older = the oldest third of the sample. *p < .05

The mean within- and between- valence category similarity scores for representations of positive images in the amygdala are presented for the participants with the lowest CES-D scores (n = 19, mean CES-D = 6.58, SD = 4.98) and those with the highest CES-D scores (n = 18, mean CES-D = 40.25, SD = 6.33) in Figure 10. The two

CES-D groups did not differ on within- (t = 0.97, p = .341) or between-valence (t = 1.00, p = .326) category similarity.

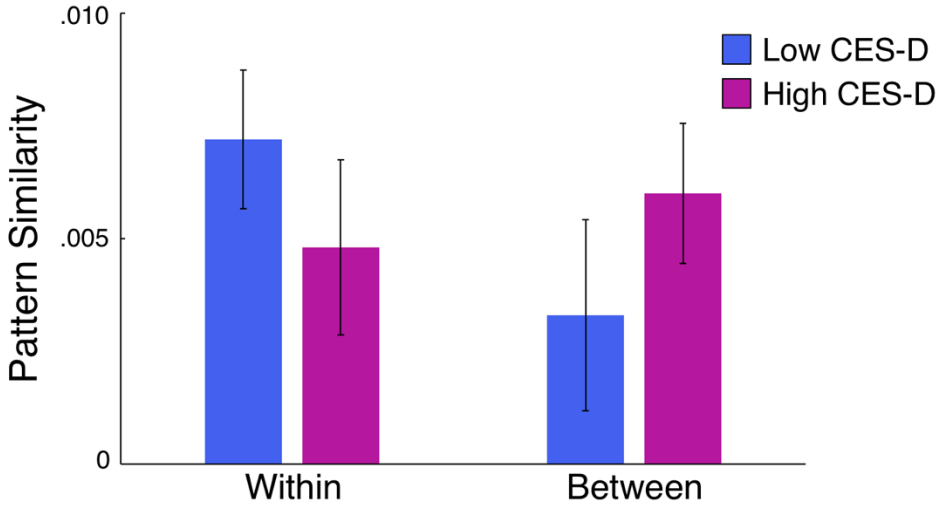

Figure 10 – Within- and Between-Valence Category Similarity for Amygdala Representations of Positive Images in Participants with the Lowest and Highest CES-D Scores

Note. Low CES-D = the third of the sample with the lowest CES-D scores, High CES-D = the third of the sample with the highest CES-D scores.

3.2.3 Functional Connectivity

3.2.3.1 Across Participants

Functional connectivity was assessed using a Valence (positive, neutral, negative) x ROI (left amygdala, right amygdala, VOTC, hippocampus) ANOVA, separately for the vmPFC and dmPFC seeds. For vmPFC, the ANOVA revealed a significant main effect of ROI, $F(2.18, 113.19) = 25.07$, $p < .001$, $\eta_p^2 = .33$; neither the main effect of valence nor the interaction was significant, Fs < 1.89, ps > .156, η_p^2s < .04. The ANOVA for dmPFC

revealed a significant main effect of ROI, $F(2.25, 123.78) = 4.94$, $p = .006$, $\eta_p^2 = .08$; as well as a significant interaction effect, $F(4.29, 216.87) = 2.58$, $p = .035$, $\eta_p^2 = .05$; the main effect of valence was not significant, $F(2, 110) = 0.06$, $p = .941$, $\eta_p^2 = .001$. To determine the source of the interaction, separate ANVOAs were conducted to compare connectivity between valence conditions within each ROI, however, none showed a significant effect of valence, Fs < 2.07, ps > .132, η_p^2s < .04.

3.2.3.2 Relationship Between Functional Connectivity and Memory Across Participants

For vmPFC, no correlations between valence condition differences in connectivity (positive – neutral, negative – neutral, negative – positive) and valence condition differences in memory discriminability or bias were significant (rs < .21, ps > .141). For dmPFC, higher positive – neutral *Pr* was associated with lower positive – neutral connectivity with left amygdala (r = -.35, p = .008); no other correlations between connectivity and *Pr* were significant (rs < .2, ps > .139). No dmPFC connectivity correlations with *Br* were significant (rs < .25, ps > .061).

3.2.3.3 Effects of Age and Depressive Symptoms on Functional Connectivity

Results are presented in Table 9. vmPFC connectivity showed significant age effects only with left amygdala: connectivity increased for positive relative to neutral and for positive relative to negative anticipation with increasing age. For dmPFC, higher CES-D scores predicted increasing positive relative to neutral connectivity with right amygdala. Older age was associated with a decrease in connectivity between dmPFC and hippocampus for negative relative to both neutral and positive anticipation. Older age was

also predictive of a decrease in connectivity between dmPFC and VOTC for negative relative to neutral anticipation, and notably, this relationship was moderated by CES-D. The simple slopes (Figure 11) reveal minimal age differences in connectivity with high depressive symptoms (+1 SD CES-D) and large age differences with low depressive symptoms (-1 SD CES-D).

Table 9 – Effects of Age and Depressive Symptoms on Functional Connectivity During Catch Trials

	Model 1			Model 2		
	B	*SE B*	*β*	*B*	*SE B*	*β*
vmPFC						
Left Amygdala						
Positive – Neutral						
Age	0.015	0.006	.343*	0.014	0.006	.330
CES-D	0.014	0.007	.275	0.014	0.007	.278
Age x CES-D	—	—	—	0	0	-.057
R^2		.139			.142	
F for ΔR^2		4.04*			0.176	
Negative – Neutral						
Age	0.002	0.006	.055	0.001	0.006	.017
CES-D	0.004	0.007	.076	0.004	0.007	.089
Age x CES-D	—	—	—	0	0	-.151
R^2		.006			.027	
F for ΔR^2		0.160			1.047	
Negative – Positive						
Age	-0.013	0.006	-.304*	-0.013	0.006	-.324*
CES-D	-0.010	0.007	-.214	-0.010	0.007	-.210
Age x CES-D	—	—	—	0	0	-.085
R^2		.101			.108	
F for ΔR^2		2.811			0.371	
Right Amygdala						
Positive – Neutral						
Age	0.006	0.005	.168	0.006	0.006	.166
CES-D	0.010	0.006	.222	0.010	0.006	.222
Age x CES-D	—	—	—	-0.00002	0	-.008
R^2		.056			.056	
F for ΔR^2		1.480			0.003	
Negative – Neutral						
Age	0.001	0.004	.020	0	0.005	-.004
CES-D	0.0001	0.005	.001	0	0.005	.010

Age x CES-D	—	—	—	0	0	-.096
R^2		0			0.009	
F for ΔR^2		0.010			0.422	
			Negative – Positive			
Age	-0.006	0.005	-.148	-0.006	0.006	-.165
CES-D	-0.010	0.006	-.215	-0.009	0.006	-.209
Age x CES-D	—	—	—	0	0	-.067
R^2		.050			.054	
F for ΔR^2		1.309			0.216	
			VOTC			
			Positive – Neutral			
Age	0.002	0.008	.036	0.002	0.008	.040
CES-D	0.00002	0.009	0	-0.00005	0.009	-.001
Age x CES-D	—	—	—	0.00005	0	.014
R^2		.001			.001	
F for ΔR^2		0.033			0.008	
			Negative – Neutral			
Age	-0.003	0.008	-.060	-0.002	0.008	-.036
CES-D	-0.001	0.009	-.018	-0.002	0.009	-.027
Age x CES-D	—	—	—	0	0.001	.098
R^2		.003			.012	
F for ΔR^2		0.084			0.437	
			Negative – Positive			
Age	-0.005	0.009	-.089	-0.004	0.009	-.069
CES-D	-0.001	0.010	-.017	-0.002	0.010	-.024
Age x CES-D	—	—	—	0	0.001	.079
R^2		.007			.013	
F for ΔR^2		0.186			0.284	
			Hippocampus			
			Positive – Neutral			
Age	0.002	0.004	.085	0.001	0.004	.059
CES-D	0	0.004	.014	0.001	0.004	.023
Age x CES-D	—	—	—	0	0	-.105
R^2		.007			.017	
F for ΔR^2		0.171			0.503	
			Negative – Neutral			
Age	-0.004	0.003	-.163	-0.004	0.003	-.194
CES-D	-0.001	0.004	-.033	-0.001	0.004	-.022
Age x CES-D	—	—	—			
R^2		.025			.039	
F for ΔR^2		0.631			0.712	
			Negative – Positive			
Age	-0.006	0.004	-.205	-0.006	0.004	-.208
CES-D	-0.001	0.005	-.038	-0.001	0.005	-.038
Age x CES-D	—	—	—	-0.00001	0	-.004
R^2		.039			.039	

F for ΔR^2		1.009			0.001	
dmPFC						
Left Amygdala						
		Positive – Neutral				
Age	-0.003	0.006	-.066	-0.003	0.006	-.079
CES-D	0.005	0.007	.094	0.005	0.007	.095
Age x CES-D	—	—	—	0	0	-.063
R^2		.017			.021	
F for ΔR^2		0.463			0.199	
		Negative – Neutral				
Age	-0.006	0.006	-.141	-0.007	0.006	-.157
CES-D	0.010	0.007	.201	0.010	0.007	.202
Age x CES-D	—	—	—	0	0	-.078
R^2		.078			.084	
F for ΔR^2		2.250			0.328	
		Negative – Positive				
Age	-0.003	0.006	-.078	-0.004	0.006	-.082
CES-D	0.005	0.007	.112	0.006	0.007	.112
Age x CES-D	—	—	—	-0.00005	0	-.017
R^2		.024			.024	
F for ΔR^2		0.655			0.015	
Right Amygdala						
		Positive – Neutral				
Age	0.006	0.005	.159	0.006	0.006	.162
CES-D	0.016	0.006	.345*	0.016	0.006	.345*
Age x CES-D	—	—	—	0.00004	0	.015
R^2		.109			.109	
F for ΔR^2		3.25*			0.012	
		Negative – Neutral				
Age	0.001	0.006	.028	0.001	0.007	.034
CES-D	0.009	0.007	.178	0.009	0.007	.177
Age x CES-D	—	—	—	0.0001	0	.026
R^2		.029			.030	
F for ΔR^2		0.796			0.034	
		Negative – Positive				
Age	-0.005	0.006	-.113	-0.005	0.007	-.111
CES-D	-0.007	0.007	-.131	-0.007	0.007	-.131
Age x CES-D	—	—	—	0.00003	0	.012
R^2		.020			.021	
F for ΔR^2		0.551			0.008	
VOTC						
		Positive – Neutral				
Age	-0.004	0.008	-.078	-0.003	0.008	-.065
CES-D	0.006	0.009	.093	0.006	0.009	.092
Age x CES-D	—	—	—	0	0	.058
R^2		.019			.023	

F for ΔR^2		0.522			0.173	
		Negative – Neutral				
Age	-0.024	0.009	-.358*	-0.020	0.009	-.301*
CES-D	-0.008	0.010	-.100	-0.008	0.010	-.105
Age x CES-D	—	—	—	0.001	0.001	.266*
R^2		.115			.182	
F for ΔR^2		3.444*			4.273*	
		Negative – Positive				
Age	-0.020	0.009	-.299*	-0.017	0.009	-.252
CES-D	-0.013	0.011	-.175	-0.014	0.010	-.179
Age x CES-D	—	—	—	0.001	0.001	.221
R^2		.086			.133	
F for ΔR^2		2.502			2.792	
		Hippocampus				
		Positive – Neutral				
Age	-0.002	0.004	-.061	-0.003	0.004	-.099
CES-D	0.005	0.005	.137	0.005	0.005	.141
Age x CES-D	—	—	—	0	0	-.179
R^2		.028			.058	
F for ΔR^2		0.760			1.677	
		Negative – Neutral				
Age	-0.011	0.004	-.350*	-0.011	0.004	-.358*
CES-D	-0.002	0.005	-.069	-0.002	0.005	-.068
Age x CES-D	—	—	—	-0.0001	0	-.033
R^2		.112			.113	
F for ΔR^2		3.346*			0.063	
		Negative – Positive				
Age	-0.009	0.004	-.291*	-0.008	0.004	-.261
CES-D	-0.007	0.005	-.200	-0.007	0.005	-.203
Age x CES-D	—	—	—	0	0	.138
R^2		.087			.106	
F for ΔR^2		2.536			1.058	

*$p < .05$

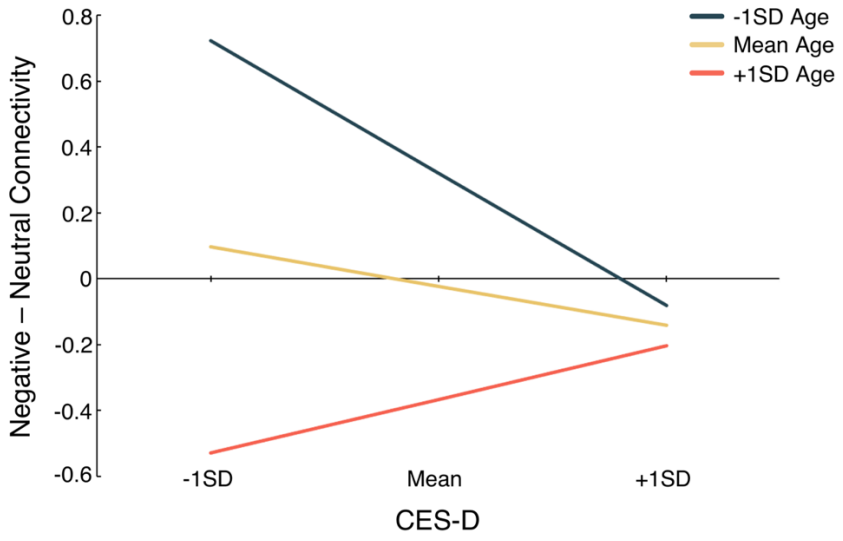

Figure 11 – Simple Slopes for Negative – Neutral Functional Connectivity Between dmPFC and VOTC

CHAPTER 4. DISCUSSION

Age-related positivity effects and depression-related mood congruency effects have been well established in the literature. What is less well understood is how depressive symptoms throughout the adult lifespan differentially influence emotional memory and the underlying neural processes. With this dissertation, I sought to determine whether depressive symptoms in older age diminish the behavioral and neural correlates of the positivity effect that is often exhibited in healthy aging. Despite the COVID-19 pandemic severely limiting data collection, I amassed a sample of 56 participants ages 18-76 with a range of depressive symptom severity to investigate this research question. Although age was negatively correlated with symptom severity, older participants with higher levels of depression were present in the sample. Consistent with previous studies, participants in the current sample exhibited some behavioral and neuroimaging evidence of positivity effects with older age and mood-congruency effects with higher levels of depression. Additionally, the data provided support for the hypothesis that depressive symptom severity can reduce age-related positivity effects in certain instances. These findings are discussed in detail below.

4.1 Age-Related Positivity Effects

Controlling for depression, age was associated with reductions in experienced arousal, as measured by participants' intensity ratings, of negative relative to neutral images. This finding is consistent with the idea that older adults are better able than their younger counterparts to employ effective emotion regulation strategies. Previous research has shown that compared to younger adults, older adults are less likely to engage with

negative stimuli (Livingstone & Isaacowitz, 2015) and more likely to use positive reappraisal (Phillips et al., 2008; Shiota & Levenson, 2009) to reduce negative affect. In the current study, age showed a marginal positive relationship with the ERQ reappraisal measure when controlling on CES-D (β = .263, p = .051), suggesting a trend of older age being associated with increased use of reappraisal in everyday life. However, in the encoding task, participants were not trained on, nor were they instructed to use, specific emotion regulation strategies. It is therefore unclear whether the strategies measured in the ERQ were implemented in the task. While the post-scan survey did ask about participants' use of various strategies, no relationships with age were significant. That said, there are a few reasons these null results should be interpreted with caution. 1.) Questions on the ERQ tap into daily life where mood tends to vacillate from situation to situation. The post-scan survey, on the other hand, was quite specific, asking about tactics used during the encoding task. 2.) It is unclear what criteria participants used when they made their decisions about the frequency of use for each strategy. There are likely individual differences in how accurately participants reported on their strategy use. 3.) Several participants sought clarification on the survey questions, particularly the questions about dampening emotional reaction and reinterpreting the meaning of images. It is certainly possible that other participants were also unaware of what the question was asking and, instead of seeking clarification, they simply responded with "never". These factors make comparisons with emotion regulation studies difficult because it is the norm in those studies to train participants on the strategies in advance of task completion and to explicitly ask them to implement those strategies during the task (e.g., Livingstone & Isaacowitz, 2018; Scheibe et al., 2015; Silvers et al., 2017). However, the imaging data lend support to the argument

that older age was associated with increased use of regulation strategies during the task, as discussed below.

Lower amygdala activation for negative – neutral trials with older age is supportive of the positivity effect. This finding is consistent with previous literature showing reduced amygdala activity for older compared to younger adults for negative facial expressions (Fischer et al., 2010; Fischer et al., 2005; Tessitore et al., 2005) and negative images (Leclerc & Kensinger, 2011; Mather et al., 2004). As noted in a prior review (Mather, 2016), the amygdala shows minimal structural changes with age and still activates in response to emotional material, but there is a shift in responsiveness to positive over negative valence. One possible explanation for this shift is changes in emotion regulation processes with age. The SST posits that perceptions regarding time remaining in life can influence individuals to place greater emphasis on emotional wellbeing as they age (Carstensen et al., 2006). At the neural level, negative emotion regulation can take the form of increased medial PFC activity and resulting decrease in amygdala activity (Motzkin et al., 2015; for review, see Nashiro et al., 2012). In the current study, functional connectivity analyses revealed lower coupling between vmPFC and left amygdala for negative – positive catch trials and greater coupling for positive – neutral catch trials with age. That is, more recruitment of vmPFC was associated with less amygdala recruitment for negative versus positive catch trials and increased amygdala recruitment for positive versus neutral catch trials with older age. This finding may represent downregulation, or dampening, of negative affect and upregulation, or enhancement, of positive affect during the anticipation period (i.e., after a cue indicated the valence of the upcoming stimulus but before the stimulus was displayed). Notably, this is mostly consistent with the previous study from

our lab; though Corbett et al. (2020) did not use positive images, they nonetheless demonstrated an inverse relationship between the same vmPFC seed used in the current study and amygdala for negative versus neutral trials in older but not younger participants.

Findings in the current study also showed that older age was associated with lower coupling between dmPFC and hippocampus for negative – neutral and negative – positive catch trials. This finding is consistent with prior work showing age-related differences in dmPFC-hippocampal connectivity for negative events (Ford & Kensinger, 2018). Functional coupling between dmPFC and hippocampal activity has been associated with emotion-related semantic elaboration during episodic encoding (Kaneda et al., 2017). The finding of an inverse relationship between dmPFC and hippocampus engagement could suggest that older participants were engaging regulatory processes when anticipating negative events to reduce processing of, and thus memory for, these upcoming events. While the behavioral data did not show an effect of age on memory discriminability for negative relative to positive or neutral stimuli (when controlling on CES-D; there were, however, interactive effects between age and CES-D, which are discussed below), the relationship between age and negative – neutral intensity ratings does suggest these regulatory processes may have contributed to a reduction in experienced negative affect in response to the images.

4.2 Depression-Related Mood Congruency Effects

Across age, higher CES-D scores predicted lower reported use of reappraisal as an emotion regulation strategy in everyday life. Reappraisal—generally considered to be an effective emotion regulation strategy (Hu et al., 2014)—is used less frequently with

increasing depressive symptoms (for review, see Dryman & Heimberg, 2018). Lower use of effective strategies like reappraisal and increased use of maladaptive strategies like repetitive negative thinking have been shown to contribute to prolonged depressive affect and negative cognitive biases in depression (Everaert & Joormann, 2020). However, in the current sample, CES-D was not associated with differences in reported use of strategies on the post-scan survey (though see the previous section for a discussion of caveats of the post-scan survey) or with memory biases for negative over positive or neutral images when collapsed across age.

The lack of evidence for negative memory benefits with higher levels of depression when controlling on age was somewhat unexpected. There was, however, an interactive effect between CES-D and age in predicting memory differences between valence conditions, which is discussed in the next section. Mood-congruency effects are quite common in the depression literature (Bower, 1981; Marchetti et al., 2018; Matt et al., 1992; Van Vleet et al., 2019), though they are not always found (e.g., Olsen et al., 2015; Ridout et al., 2009; Toki et al., 2014). Inconsistencies may relate to the characteristics of the task or characteristics of the individuals taking part in the study. For example, Gotlib and Joormann (2010) noted that free recall tasks produce the most consistent evidence of negative memory biases in depression, while recognition tasks are not as consistent. Others have found biases on incidental but not intentional memory tasks (Direnfeld & Roberts, 2006). Another factor may be how the material is encoded, with self-referencing producing larger memory benefits for negative material in depression than non-self-referencing. Furthermore, effects of depression on memory are larger in individuals with diagnosed major depressive disorder than in those with subthreshold depression (for review and meta-

analysis, see James et al., under review). In the current study, a heterogenous sample of participants (in terms of age and depressive symptoms) completed an intentional recognition task with no explicit instructions to encode the material in a self-referential manner. It is therefore perhaps unsurprising to find a lack of evidence for traditional mood-congruency effects in the form of individuals with higher levels of depression across age exhibiting better memory for negative and worse memory for positive or neutral images.

Often accompanying the negative memory benefits common in depression are differential amygdala responses to stimulus valence. That is, compared with controls, those with clinical depression tend to show amygdala hyperactivation for negative stimuli and hypoactivation for positive stimuli (for meta-analysis and review, see Groenewold et al., 2013). In the current study, higher CES-D score was associated with a reduction in positive versus neutral amygdala activity, but also a reduction in negative versus neutral amygdala activity. Lower amygdala activity in depression is not entirely at odds with previous research. For example, in one study (Ferri et al., 2017) where participants labeled the emotion displayed on face stimuli (i.e., affect labeling of happy and sad faces), those with depression exhibited blunted amygdala responses relative to healthy controls, and this blunted response was related to higher symptom severity. Similarly, Benning and Ait Oumeziane (2017) provided evidence for underarousal in subclinical depression, such that higher symptoms of depression were associated with lower physiological response to emotional images. Thus, the finding of lower amygdala response for emotional images in the current study is not unprecedented.

Connectivity results showed greater coupling between dmPFC and right amygdala for positive than neutral catch trials for participants with higher CES-D scores across age.

It should be noted that a positive, yet nonsignificant, relationship existed for negative relative to neutral catch trials. While increased connectivity between dmPFC and amygdala has been linked to upregulation of positive affect (Scharnowski et al., 2020), it seems unlikely that is the case here, as depression is frequently associated with decreased ability to upregulate positive emotions (for review, see Carl et al., 2013). Using a similar experimental design to that used in the current study where young participants saw a valence cue then an emotional or neutral image, Zhang et al. (2017) found that compared to healthy controls, depressed participants showed greater dmPFC connectivity with posterior cingulate cortex (PCC) and parieto-occipital cortex during anticipation of positive relative to neutral images. Healthy controls showed inverse connectivity between these regions, which was believed to reflect disengagement of distracting thoughts to direct attention to the upcoming stimulus. The authors suggested the dysfunctional connectivity in depression could reflect failure to shift focus from internal thoughts to the external environment, resulting in impaired attention for positive events. Difficulty disengaging from internal, or self-focused, thoughts is a pattern associated with rumination, which is known to contribute to onset and maintenance of depressive symptoms (for review, see Watkins & Roberts, 2020). In the current study, inverse connectivity was more common among those with lower levels of depression while greater connectivity was more common with higher levels of depression for positive relative to neutral catch trials across age (see Figure 12 in Appendix). These pre-stimulus connectivity patterns are consistent with the idea that those with greater depressive symptoms are more likely to engage in rumination, making it difficult for them to disengage from internally directed thought and thus contributing to reduced attentional orienting. The finding that this pattern was less

pronounced during negative catch trials suggests negative cues may have been more salient than positive cues—not enough to eliminate rumination for negative trials, but enough to reduce the effect. Although behavioral results did not show higher CES-D to be associated with lower positive versus neutral memory discriminability, the possibility that greater symptom severity contributed to reduced preparatory processing of positive stimuli cannot be ruled out.

4.3 Interactive Effects Between Age and Depressive Symptoms

With low levels of depressive symptoms, positive – neutral memory discriminability was essentially equivalent across age and depressive symptoms. This finding may seem at odds with the idea of the positivity effect, in which one might expect that the difference between positive and neutral would increase with age. However, a meta-analysis (Reed et al., 2014) found that older adults' bias for positive information is most consistently observed when their processing resources are unconstrained versus constrained. For example, positivity bias effects are larger when participants passively view the to-be-remembered material and smaller when they are directed to operate on the stimuli. In the current study, participants were asked to make intensity judgments about the images. Carstensen and DeLiema (2018) suggest that passive viewing of experimental stimuli does not interfere with the activated goals that, according to the SST, differ for younger and older adults. Requiring participants to actively engage with the material, on the other hand, essentially assigns new goals that may override, at least temporarily, the goal of older adults to prioritize positive information.

At low levels of depressive symptoms, older participants did show reduced memory discriminability for negative material compared to younger participants. This finding is consistent with the positivity effect in healthy aging. Indeed, many studies have not necessarily shown a memory benefit for positive material in older age but rather a reduced memory benefit for negative material (Charles et al., 2003; Gruhn et al., 2007; Leclerc & Kensinger, 2011; but see Reed et al., 2014). It is important to note, however, that a majority of studies investigating the positivity effect have been conducted on samples without depression. In the present study, behavioral results showed that when depressive symptoms started to be a factor, there was a reversal in the pattern of age effects such that older participants with higher CES-D scores show greater negative memory benefits than young and middle-aged adults and older adults with low CES-D scores. This suggests that higher levels of depression in older adults are associated with weakened positivity effects in memory discriminability.

An unexpected finding is that for younger participants, higher level of depression was associated with worse memory for negative relative to neutral images. Mood congruency would suggest improvements in memory for negative material with increasing levels of depression. One possibility for this result is that younger adults with higher depressive symptoms may be more apathetic and thus do not find the emotional images as arousing. As established in the current study and others (e.g., Dolcos & Cabeza, 2002; Mather & Sutherland, 2011; McGaugh, 2018), arousal plays an important role in memory salience. Emotional images may have not been as arousing for younger depressed participants as they were for older participants or those with lower levels of depression. In turn, this may have contributed to younger, high-depression participants showing minimal

memory differences between negative and neutral images. Anhedonia has been associated with reduced emotional experience (Mathews & Barch, 2006) and with reduced emotional memory for negative material (Olsen et al., 2015). While the current study did not show that anhedonia symptoms as measured by the CES-D were correlated with age (r = -.09, p = .492), it is possible that the two anhedonia questions on the CES-D were insufficient to measure trait anhedonia. To further explore this question, future studies may wish to include more extensive measures of anhedonia, such as the Physical and Social Anhedonia Scales (Chapman et al., 1976), Dimensional Anhedonia Rating Scale (Rizvi et al., 2015), or others (for review, see Rizvi et al., 2016).

Interactive effects of age and depressive symptoms are also be seen in the univariate results. The finding that positive – neutral VOTC activity decreased with increasing depressive symptoms in older adults suggests that at low levels of depression, older participants demonstrated a positivity effect in neural recruitment of perceptual processing regions. That is, inferior occipital and temporal areas showed more activity during the processing of positive trials than during the processing of neutral trials. This finding is consistent with previous work showing higher positive versus neutral BOLD signal in perceptual processing regions in healthy older adults than in younger adults (Kehoe et al., 2013). However, with increasing levels of depression, this positivity effect was reduced in older individuals, such that engagement of these visual processing regions during positive trials looked more like that during neutral trials. This suggests that higher level of depression in older age reduces the preferential perceptual processing of positive material that is found in healthy aging. Depressive symptoms were not as much of a factor for

younger participants' positive – neutral VOTC activity, suggesting level of depression did not strongly impact perceptual processing of positive material in younger individuals.

Finally, the relationship between CES-D and negative – neutral functional connectivity between dmPFC and VOTC was moderated by age. Older participants with low levels of depression demonstrated evidence of suppression of negative affect. That is, when cues indicated an upcoming negative image, compared to low-depression younger participants, low-depression older participants showed lower connectivity between dmPFC and VOTC than when cues indicated an upcoming neutral stimulus. The strength and vulnerability integration (SAVI) model (Charles, 2010) suggests that older adults are able to maintain positive emotional states by employing regulation strategies prior to the onset of a negative stimulus. By providing valid cues to signal the valence of the upcoming stimulus, the experimental paradigm used in the current study allowed older adults to engage the necessary strategies to reduce negative affect. However, as mentioned above, participants were not instructed to use any specific strategies—emotion regulation or otherwise—during the encoding task. Corbett et al. (2020) previously showed that healthy older adults spontaneously downregulated negative affect when anticipating a negative image. This downregulation was accomplished via medial PFC exerting top-down control to reduce activity in several regions including those important for perceptual processing and memory encoding (e.g., inferior occipital, parahippocampal gyrus). Notably, this effect was absent in the young adults. However, it was unclear from their study whether these differences between age groups were in fact due to age or were due to their young adults having higher levels of depressive symptoms than the older adults. Findings in the current study elucidate this uncertainty by showing that at low levels of depression, older age was

associated with reduced connectivity. With increasing levels of depression, however, this age effect was greatly reduced. This suggests that depressive symptoms interfere with older adult's ability to spontaneously engage regulation processes to suppress activity in perceptual processing regions in the face of impending negative stimuli. This finding is consistent with the idea that depression interferes with successful emotion regulation (Pico-Perez et al., 2017).

Interestingly, increasing depressive symptoms in younger participants were associated with a decrease in dmPFC-VOTC connectivity during negative versus neutral catch trials. Previous research has shown dysfunctional connectivity in young patients with depression during anticipation of negative stimuli, suggestive of enhanced bottom-up perceptual processing co-occurring with attenuated top-down regulatory processing (Manelis et al., 2016; Strigo et al., 2013). Feeser et al. (2013) linked reduced prefrontal responses during emotional anticipation in depressed individuals versus controls to environmental disengagement associated with increased apathy or loss of motivation that is characteristic of depression. This account provides a link to the behavioral finding in the current study of reduced memory discriminability for negative relative to neutral images in younger participants with higher levels of depression. Higher levels of apathy in these individuals may contribute to impaired anticipatory processing that ultimately hurts their ability to effectively encode and subsequently retrieve the information. Future studies may wish to include a better measure of anhedonia to test the role apathy plays in emotional expectancy and encoding in depression.

4.4 RSA

The RSA results did not clearly fit into the previous sections on positivity effects or mood congruency effects but are nonetheless worthy of discussion. Older age was associated with reduced category specific representation of certain valence conditions in certain ROIs. The conceptualization of CSR involved determining how much the neural pattern of activity associated with trials from one valence category resembled that of other trials from that same valence category (within-category similarity) compared to that of trials from a different valence category (between-category similarity). Decomposing the CSR estimate to examine how these two elements were impacted by age revealed that lower CSR estimates tended to be the result of lower within-category similarity with age, not higher between-category similarity. Previous research has shown that aging is associated with reductions in distinctiveness of neural patterns, and this neural dedifferentiation is central to age-related declines in episodic memory (Kobelt et al., 2021). The current findings are somewhat consistent with prior work showing reduced within-category similarity in older adults (Carp et al., 2011; Trelle et al., 2019), though these studies also showed higher between-category similarity in their older participants. As suggested in a recent review (Sommer & Sander, 2021), higher within-category and lower between-category similarity may often benefit memory performance. The aim of the current study was to investigate how age and depressive symptoms contributed not to overall memory performance, but rather to relative memory benefits for one valence category over another. Thus, while it was not a focus of this study, lower CSR estimates with age could be related to lower memory discriminability across valence. This possibility should be explored in future investigations.

Interestingly, the effect of CES-D on positive CSR in the OFC was moderated by age. In older participants, increasing depression was associated with decreasing CSR, such that those with high levels of depression showed CSR values indicating greater between- than within-category similarity for positive stimuli. Although research investigating the effects of depression on pattern similarity is currently lacking, age-related reductions in within-category pattern similarity have been linked to older adults' deficits in memory performance, as discussed above. Previous work (Chikazoe et al., 2014) has indicated that activation patterns within the OFC can represent unique valence experiences (for review, see Kragel & LaBar, 2016). It is possible that OFC patterns in the highly depressed older adults are indicative of diminished ability of the OFC to reliably distinguish positive from neutral events, though this did not appear to impact memory performance, as age did not significantly moderate the relationship between CES-D and positive – neutral *Pr*. In younger participants, higher level of depression was associated with higher positive CSR. If higher CSR is related to memory benefits for the represented valence category, this finding would seemingly be inconsistent with the literature showing reduced memory benefits for positive information in depression (Dillon & Pizzagalli, 2018; though notably this pattern was not found in the current study for younger participants). One possibility is that greater pattern similarity represents encoding of category-level details (Zeithamova et al., 2019) that does not necessarily improve subsequent recognition of specific stimuli. However, in the absence of analyses to determine how age, depressive symptoms, and pattern similarity interactively affect memory performance, the possibilities discussed here remain purely speculative.

4.5 Limitations

The small sample size was a significant limitation of the study. Post-hoc power analyses suggested some marginal expected effects required a sample size of around 105 participants to reach significance. From the outset, the goal was to collect usable data from 75-100 participants. This goal likely would have been attainable had data collection not been halted from March through November 2020 due to the COVID-19 pandemic. An additional limitation was the age distribution of the sample. Recruiting older participants became particularly challenging once data collection resumed. As a result, the final sample not only skewed young, but higher levels of depression were more common in younger ages. That is not to say that higher levels of depression were absent in older participants. Among the 10 subjects over the age of 60, CES-D scores ranged from 0-35. However, age and CES-D were negatively correlated. Though these predictors were centered for all regression analyses to reduce multicollinearity, it could not be eliminated, and thus likely reduced the power of the regression models.

Another limitation of the small sample size is that I was unable to relate the age and depressive effects on imaging measures to memory performance. Such an analysis would involve including age, CES-D, and imaging measure (e.g., univariate activity differences between valence conditions) as predictor variables within the same model, in addition to interaction terms between these variables, to predict memory outcome. While the current sample did allow me to identify several instances where age moderated the relationship between CES-D and either memory or underlying neural indices, a significantly larger sample would be needed to determine whether these variables interactively influenced subsequent memory.

Finally, the heterogenous sample was both a limitation and a strength of the study. By recruiting adult participants of all ages with a range of depressive symptom severity, I was able to test the unique and interactive effects of these two variables for predicting emotional memory performance. However, including some individuals who were diagnosed with MDD and some who were receiving treatment (either medication, therapy, or both) may have attenuated some effects. In a recent meta-analysis (James et al., under review), I found episodic memory deficits were more pronounced in those with diagnosed depression than in those with subthreshold depression compared to healthy controls, and deficits were largest in studies where a greater proportion of depressed participants were receiving pharmacological treatment at the time of study. Though diagnosis was not found to specifically impact emotional memory in the meta-analysis, the impact of treatment on emotional memory could not be tested due to sample size limitations. Future studies may wish to take these factors into consideration when recruiting participants.

4.6 Conclusions

The current study provides novel supporting evidence for the hypothesis that the positivity effect in memory exhibited in healthy aging is reduced in adults with depressive symptoms. This reduction coincides with alterations in neural recruitment of a network of regions underlying emotion regulation. These neural findings suggest that successful downregulation of negative affect in older age is reduced with higher levels of depression. This study is the first to show interactive effects of age and depressive symptoms on the positivity effect in memory and the associated neural mechanisms involved in anticipating and responding to emotional events. Although a relatively small sample size limited some analyses, the findings presented here underscore the importance of investigating depressive

symptoms throughout adulthood. This study lays the groundwork for future individual differences research to continue exploring these relationships and their associated factors (i.e., treatment, medication, sex) in larger samples.

APPENDIX

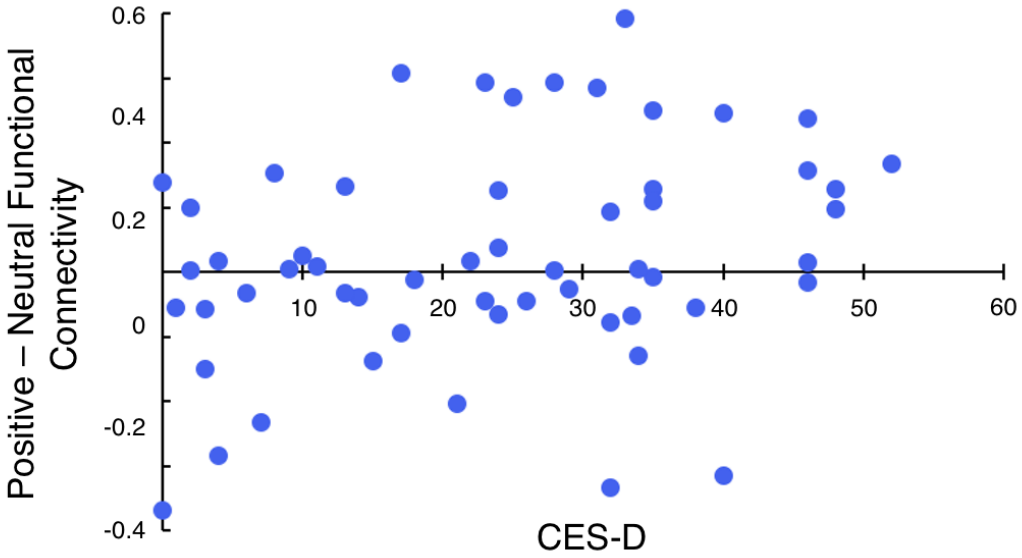

Figure 12 – Relationship Between CES-D and dmPFC-Right Amygdala Functional Connectivity for Positive – Neutral Catch Trials

Note. Results in the figure are presented across age. When controlling on age, CES-D: $\beta =$ .345, $p = .015$.

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